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# You, Us & Them:

From motor simulation to  
ascribed shared intentionality  
in social perception

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From motor simulation to  
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in social perception

## **Proefschrift**

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# Contents

Chapter 1	General Introduction	9
Chapter 2	<i>You</i> : Does impairment in action execution impair perception of individual actions?	25
Chapter 3	<i>You</i> : Do the motor specific parameters of an observed action engage the motor system?	45
Chapter 4	<i>Us</i> : Does sharing tasks affect memory encoding?	69
Chapter 5	<i>Them</i> : Does ascribed shared intentionality modulate neural processing of observed social interactions?	85
Chapter 6	Summary & General Discussion	113
	References	127
	Nederlandse Samenvattig	149
	Curriculum Vitae	153
	Publications	155
	Acknowledgments	157
	Donders Series	161



## Chapter 1

# General Introduction

We are social animals. But, so are penguins. However, unlike us, penguins don't make Turkish delight, or any other dessert for that matter. Turkish delight may or may not be to everybody's taste, but it is one of the things that make human sociality unique. Like pagan rituals, computer software, alphabets, divorce law, and presidential campaigns, it is the product of a sophisticated cumulative process that is cooperative in essence. It takes a multitude of individuals engaging in a series of intricately complex interactions to develop a recipe and to carry it over generations. Cooperation is, perhaps, the most outstanding feature of human sociality.

Collaborative pursuits of joint outcomes require that individuals need to have their respective intentions and action plans interlocked. How does individual social cognition support such an interlocking? How do the dynamics of social interactions exploit and constrain individual cognitive mechanisms? Perhaps most crucially, how do individuals explain and anticipate each other's behaviour? These questions canvass the general theme of this thesis.

The question of how we make sense of others' behaviour has long been a focus of developmental enquiries of social cognition. Theory of Mind (ToM) (Premack & Woodruff, 1978), the ability to ascribe mental states (e.g. false beliefs; Wimmer & Perner, 1983) to others has widely been studied in human infants and adults (for a review, see Frith & Frith, 2003) emphasizing the role of explicit reasoning in social cognition and social interaction. Research in Cognitive Neuroscience has since identified a cortical network in the human brain that is involved in ToM reasoning. Furthermore, recent inquiries have accumulated a considerable body of evidence demonstrating that human infants, as well as some non-human species, have a capacity to efficiently process beliefs and other mental states, suggesting an implicit form of mentalizing that bypasses conceptual explicit reasoning (for an overview, see Apperly & Butterfill, 2009). For example, it has been shown that we can efficiently and effortlessly compute others' visuo-spatial perspectives (Samson, Apperly, Braithwaite, Andrews & Scott, 2010) belief-like states (Kovacs, Teglas &

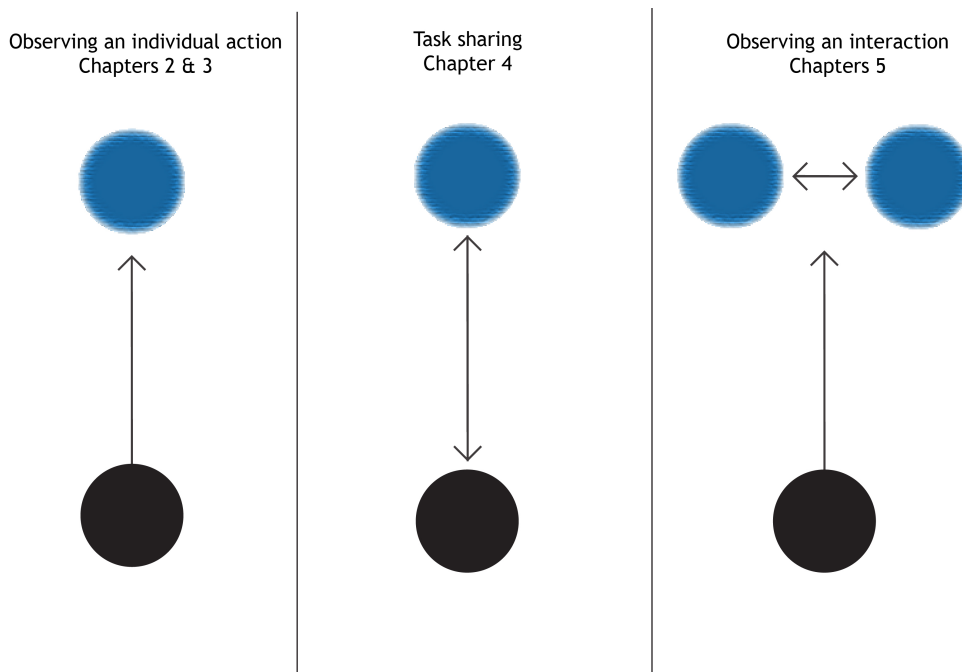
Endress, 2010), or tasks (Sebanz, Knoblich & Prinz, 2003). Thus, sometimes we know what others know, believe or intend without a cost to our cognitive resources. Mentalizing processes help us to derive the most likely reasons behind others' behaviours.

With the recent popularity of embodied approaches to social cognition, basic perception action links (Jeannerod, 1999) have gained prominence as non-conceptual means for interpersonal connections, providing yet another way to think about social cognition. In the action domain, perception action coupling has been implicated in simulations of observed actions that recruit the observer's motor system (Decety & Grezes, 2006). Behavioural evidence in support of this claim reveals that action simulations service explaining and predicting others' actions (Wilson & Knoblich, 2005). Neurophysiological studies have identified a cortical network in the human brain that resonates with, or 'mirrors', the actions one observes (for a recent review, see Rizzolatti & Sinigaglia, 2010). A similar mirroring mechanism leads to resonance of others' sensations and emotions, and offers a non-conceptual account to empathy (de Vignemont & Singer, 2006).

Thus there are different types of cognitive and neural mechanisms that allow us to establish interpersonal connections and to gain epistemic access to the minds of one another. These include mentalizing (ToM) and action simulation. This list is by no means exhaustive, nor are its items mutually exclusive. Different aspects of social cognition require different types of processes that may or may not be active at the same time. These processes range from symbolic thought to sensorimotor computations and they work in remarkable harmony to allow us to perceive and understand the actions, goals and mental states of individuals we encounter and the social interactions they engage in with other people. Central to this thesis is the question of how individual cognitive and neural processes support perception and understanding of others' behavior. The following chapters describe four studies that investigated social perception processes by employing three different forms of social interactions or social contexts (Figure 1.1): observing an individual's actions,



interacting with another individual to jointly perform a task, and observing an interaction. Specific questions addressed in each chapter are as follows. Do individual motor processes and their neural correlates contribute to perception of another individual's action (Chapter 2 and 3)? How do thought processes exploit and constrain the sensorimotor system to support social interactions; and, how are thought and memory processes influenced by the requirements of social interactions (Chapter 4)? How are mentalizing and action perception processes recruited when ascribing intentional relations to observed social interactions and what are the associated cortical regions (Chapter 5)?



**Figure 1.1:** The different social contexts addressed in this thesis. Black circles represent the observing agent (the participant), blue circles represent the observed agents.

## **Observing you: Perception-action matching and motor simulation**

A vast amount of evidence has accumulated over the last two decades that speaks for the claim that perception and action are tightly linked through common underlying representations (Jeannerod, 2001; Prinz, 1997). Accordingly, perceived actions are matched with action representations that are part of the observer's motor repertoire. Extending on early theories of voluntary action control (ideomotor theory; James, 1890) common coding theory postulates that actions are specified in terms of their distal perceptual effects (Hommel, Muesseler, Ascherlsleben & Prinz, 2001; Prinz, 1997). These perceptual effects are assumed to activate a corresponding representation in the observer, leading to "motor resonance". In other words, common codes act as an interface between perception and action, thus implying functional equivalence between motor representations for actions and for perceptions.

To illustrate, when my friend pours water into a pot as she starts making Turkish delight, the trickling sound of the water against the metal surface triggers in my motor system previously acquired action representations that are associated with the action of pouring water. Thus the assumption of common coding predicts that perceiving another perform an action should facilitate executing the perceived action because it results in an activation of motor representations. Indeed, individuals are more likely to be faster at performing a particular movement when they watch somebody perform the same movement than when they watch the person perform a different movement (Brass, Bekkering & Prinz, 2001; Kilner, Paulignan & Blakemore, 2003; Bach & Tipper, 2007).

Evidence from neurophysiological studies suggests that a common coding system is implemented at a neuronal level. Mirror neurons, initially discovered by single-cell studies on the macaque brain (di Pellegrino, Fadiga, Fogassi, Gallese & Rizzolatti, 1992; Gallese, Fadiga, Fogassi & Rizzolatti, 1996) offer a neural substrate of common coding through which perception and action become coupled (for a review, Rizzolatti & Sinigaglia, 2010). Mirror neurons are essentially motor neurons

(involved in action production) that also respond to perceived movements. In other words, they map perceived actions to executable motor representations. A wealth of neurophysiological studies indicates the presence of an analogous mirroring circuitry in the human brain. Comprising motor areas that are involved in execution of actions (i.e. premotor cortex, inferior parietal lobule and the superior temporal sulcus) the human mirror network similarly responds to execution and observation of corresponding actions (e.g. Calvo-Merino, Glaser, Grezes, Passingham & Haggard, 2006; Hamilton & Grafton, 2006; 2008; Kilner, Neal, Weiskopf, Friston & Frith, 2009).

It has also been postulated that once a match between the observed and performed action has been established, the motor system of the observer runs simulations of the observed action as it unfolds in real time (Wilson & Knoblich, 2005). Motor simulations capitalize on internal predictive models, which comprise one's own biomechanical constraints and previously learned associations between self produced actions and their perceivable consequences (Wolpert, Doya & Kawato, 2003), and that are used to plan and execute one's own actions. Action perception exploits internal models in our motor system, allowing for accurate predictions about the likely perceptual consequences of the observed actions (Wilson & Knoblich, 2005). That is, as my friend starts moving in order to place the water filled pot on the stove I can simulate the consequences of the action and accurately predict what it will feel like to grab the plastic handle of the pot, how much effort will be needed to lift it, and where on the stove it will end up—because I have performed those actions before. However, if she was to do an acrobatic flip I wouldn't be able to predict when her feet would touch back on the ground—because, never once in my life have I managed to do a flip, and so I do not have an appropriate internal model for it.

Several research lines have empirically tested these claims. One such research line investigated the effects of motor expertise in action perception. There are now numerous studies indicating that one's level of motor skill determines the degree of

neural activation in the mirroring circuitry when observing an action that requires the same skill (e.g. Calvo-Merino et al., 2005; 2006). One's predictions concerning the outcomes of actions are also influenced by motor expertise. For example, elite basketball players outperform novices when predicting the success of basketball shoots (e.g. Aglioti, Cesari, Romani & Urgesi, 2008). These findings clearly demonstrate that perception of an action is directly linked to the motor representations that govern one's execution of an observed action. It follows that, an acquired permanent impairment in production of a movement, that has likely altered the internal models, is expected to impede one's perception of another's performance of the same movement. This hypothesis will be addressed in detail in the second chapter.

Another line of research investigated whether motor laws influence action perception. Motor laws capture physical principles that govern execution of actions. If perception and action rely on a common coding system, both execution and perception of actions should be subject to the same governing principles. Research on Fitts' law (Fitts, 1954) provides strong support for this claim. Fitts' law captures the trade-off between speed and accuracy in biological movements and combines both parameters in the index of difficulty. Fitts' law is one of the most robust principles of human motor production (Plamondon & Alimi, 1997). It has been shown in a recent study that Fitts' law also constrains the perception of movements (Grosjean, Shiffrar & Knoblich, 2007). When asked to judge whether an observed action was possible for a human to perform at a particular speed between targets of a particular size, participants complied with the law. When a perceived movement violated Fitts' law participants found the movement to be 'undoable'. These results provide direct support for the action simulation theory. Biological and physical constraints, as captured by motor laws, are encoded in one's internal models that govern one's execution of actions. When observing another performing an action, the motor system of the observer capitalizes on the same internal models, and thus poses strict and specific constraints on perception in perfect compliance to the laws.

A question this finding promotes refers to the neural correlates of motor simulations. Research on neurophysiological markers of motor resonance has largely been concerned with the degree of matching between representations of observed and representations of produced actions, and investigated the effects of general action profiles. For example, previous studies compared perception of movements with which an observer had motor familiarity to movements to which the observer was a stranger (e.g. Calvo-Merino et al., 2005; 2006). Is the motor system directly involved in simulations that incorporate detailed information regarding the motor parameters that operate during execution of actions? More specifically, do parameters that are purely motor and not directly perceivable, (e.g. effort, force or difficulty) drive the neural regions that support action production when observing others perform the same actions? Chapter 3 addresses this question.

### **Us: Task sharing and co-representation**

Perception action matching and action simulation are often thought of as involuntary processes. However, the constant need to inhibit automatic tendencies to mimic observed actions would be considerably resource consuming. Could there be top-down modulations of a general readiness to engage in action matching and action simulation? Several recent studies have identified such contextual factors that have a modulating effect on action simulation. For example, involuntary actions are not simulated (Kilner, et al., 2003; Liepelt, von Cramon & Brass, 2008; Stanley Gowen & Miall, 2007). Social relevance (Kourtis, Sebanz & Knoblich, 2010), the intentions ascribed to the observed actor (Sebanz & Shiffrar, 2009), as well as the social context of the interaction (i.e. cooperation vs. competition; Streuber, Knoblich, Sebanz, Buelthoff & de la Rosa, 2011) are other factors that have been shown to constrain action simulation. This implies that action simulation is exploited by higher-level processes that emerge at social instances that require separate representations for 'self' and for 'other' (Roepstorff & Frith, 2004), each packaged

with a different set of predictions. Sharing a task with another individual is one such instance.

When watching my friend stir a pot filled with boiling syrup, I might decide to join in and help her make the Turkish delight. In order to do so I need to coordinate my actions with her and I need to do this in a way that appropriately complements her actions so that we can achieve our now common goal. This implies the need to know the right actions my friend is supposed to perform and the need to know when she will perform these actions. For example, when she reaches for the corn flour, based on my advance knowledge of how to make Turkish delight, I can predict that she is going to add it to the boiling water. Then I can take over the stirring with the spoon to share the task. Here, action simulation can service us by allowing each of us to predict the consequence of the other's actions. However, action simulation is not all that is needed for successful completion of the task. As in prototypical cases of joint action (cf. Vesper, Butterfill, Knoblich & Sebanz, 2011) each of us needs to take into account the outcome to be achieved, our own part in the task, and the part for which the other is responsible.

A recent research line has set out to study task sharing experimentally. Recruiting paradigms that distribute across two people each half of a task, these studies suggest that individuals form representations detailing not only their own tasks but also the task for their interaction partners, even when this isn't strictly necessary. Evidence for 'shared task representations', or 'task co-representation', has been established by a wealth of studies. One of these studies (Sebanz, et al., 2003) capitalized on a known spatial compatibility effect, which creates a response selection conflict between two action alternatives when the task is performed individually (Simon, 1990). When performed by two individuals instead of one, the same compatibility effect was observed even though each individual is assigned one of the two action alternatives, and the co-actor's task was completely irrelevant for individual performance. Similar co-representation effects have been demonstrated in a number of different experimental paradigms that distributed standard tasks

used in Cognitive Psychology across two people (Simon task: Sebanz et al., 2003; Sebanz, Knoblich, Prinz & Wascher, 2006a; SNARC task: Atmaca, Sebanz, Prinz & Knoblich, 2008; Flanker task: Atmaca, Sebanz & Knoblich, 2011; Wenke, Atmaca, Hollanaender, Liepelt & Baess et al., 2011). Electrophysiological evidence corroborates the suggestion that when sharing a task individuals perform the other's task vicariously (Sebanz, et al., 1996a; Tsai, Kuo, Hung & Tzeng, 2008; de Bruijn, Miedl & Bekkering, 2008), which indicates that a co-actor's task is represented in functionally similar ways to which one's own task is represented.

The size of co-representation effects is modulated by several different factors. Affective (Hommel, Colzato & van den Wildenberg, 2009), contextual (Iani, Anelli, Nicoletti, Arcuri & Rubichi, 2011; de Bruijn, de Lange, von Cramon & Ullsperger, 2009; Ruys & Aarts, 2010) and spatial (Guagnano, Rusconi & Umiltà, 2010; Welsh, 2009; Heed, Habets, Sebanz & Knoblich, 2010) relations between task partners seem to influence the extent to which individuals take the other's task into account. One crucial requirement in forming shared representations is the co-actor's perceived intentionality. In fact, it has been demonstrated that the actual presence of an interaction partner is not always required to obtain co-representation effects; the mere belief that another person is performing another part of the task is sufficient for one actor to represent the other's task (Tsai, et al., 2008; but see Welsh, Higgings, Ray & Weeks, 2007). Conversely, if participants are led to believe that their co-actor is a computer (Tsai et al., 2008) or that the actions of the co-actor are not intentional but controlled by a machine (Atmaca et al., 2011), co-representation effects do not occur. In summary, the evidence suggests that even when two co-actors tasks are independent they take each other's part of the task into account, even when this can hurt their performance, but only if they believe that their partner is an intentional agent.

How does co-representation support coordination in social actions? Evidence indicates that having representations that specify a co-actor's part of a task govern online processes that make coordination possible. These processes include

prediction, monitoring, and stimulus processing. Advance knowledge of a co-actor's task allows us to generate accurate predictions with respect to their actions and thus with respect to ensuing interactions (Ramnani & Miall, 2003). If I know my friend is on board with making Turkish delight with me, when she reaches for the flour I can safely predict that she is going to add it to the syrup rather than batter the fish with it. Thus shared task representations, firstly help individuals generate and adjust their own actions plans in a way to complement the partner, in line with a shared goal. Secondly, it enables monitoring the success of partners' performance and identifying the mistakes they commit. Behavioural (Schuch & Tipper, 2007), neurophysiological (van Schie, Mars, Coles & Bekkering, 2004), and neuroimaging (de Bruijn et al., 2009; Newman-Norlund, Ganesh, van Schie, de Bruijn & Bekkering, 2009) evidence suggest that the neural and cognitive processes involved in monitoring our own actions are also involved when we witness others committing errors.

Together, the studies investigating the co-representation effect have provided considerable insight into the ways in which social interaction affects cognitive processes during the progression of the interaction. A still open question is whether co-representation also enhances subsequent memories related to a co-actors' task. Do I remember what brand of corn flour my friend uses even though it bears no relevance for what I have to do as we make the Turkish delight together? Research on social memory indicates that individual memory processes are susceptible to social influences (cf. Barnier, Sutton, Harris & Wilson, 2008, for an overview). For instance, it has been demonstrated that what one recalls can be subject to a reconstruction (Bartlett, 1932) that reflects what another already knows (Basden, Basden, Bryner & Thomas, 1997; Cuc, Koppel & Hirst, 2007; Coman, Manier & Hirst, 2009). This so-called 'memory conformity' (Wright & Schwartz, 2010) during retrieval resists one's will (Basden, Basden & Henry, 2000; Meade & Roediger, 2002), and is especially strong when the infectious person is physically present (ibid.). Is memory encoding susceptible to social influences as well? Particularly,



does acting together affect the way individuals encode information that is part of a co-actor's task? Chapter 4 addresses these questions.

### **Observing them: Ascribing shared intentionality**

Cooperative social interactions entail more than representing the others' actions or the tasks they are assigned to carry on. Also, the demands cooperation poses on individual cognition cannot be met by reasoning about another's mental states alone. In prototypical cases of cooperative social interactions individuals share an intention, be it to accomplish a shared goal together, or even to stay engaged in the interaction. Shared intentions serve to organize the roles individuals take on to perform their parts of a task and to mutually coordinate their actions in space and time. This is essentially different from two individuals with independent intentions, whose actions are not directed along a common pursuit (Searle, 1990). As we go about making our Turkish delight, my friend and I share the intention that we do so together. However, I do not share the same intention with her roommate who happens to be in the kitchen with us, but is making himself a pizza.

Accordingly, philosophers generally posit that the defining feature of collaborative joint actions is shared intentionality. In fact, it is the philosophical inquiries on shared intentionality have the initial interest in research on joint action (Clark, 1996). One of the resulting research lines seeks out to identify the phylogenic and ontogenic roots of cooperation. Although examples of coordinated collective activities, such as group hunting, are observed in some non-human species, theirs cannot immediately be equated to the level of sophistication human sociality demonstrates. Chimpanzees, for example, demonstrate some rudimentary forms of social understanding and collaboration (e.g. getting help to retrieve food, Melis, Hare & Tomasello, 2006). However these skills do not further develop into the level of complexity reached by the social behaviours of human infants within two years of their birth (Carpenter, 2009; Tomasello & Carpenter, 2007). The difference, it is

believed, lies in a special motivation to share affective or mental states, and engage in joint actions to achieve a common goal (Tomasello, Carpenter, Call, Behne & Moll, 2005).

How does a shared intention translate into the actualization of joint activity where individuals achieve interpersonal coordination? At first glance it seems strange to assume that groups of individuals can intend to perform an act because intentions are normally ascribed to individuals. In contrast to this intuition is the observation that groups can engage in actions that individuals alone cannot perform (Clark, 1996; Pettit, 2009). For example, a football team can win the World Cup, not individual players. A way out of this contradiction is to assume that shared intentions comprise individual intentions that are mutually interlocked (Bratman, 1992). This implies a representational structure scaffolded across individuals, and recruits cognitive processes operating at varying levels of complexity. Such a structure of shared representations orchestrates the ways in which individual behaviours, plans, goals, and intentions become coordinated (ibid.). Recursive attribution of beliefs (Tuomela, 2006, Tomasello & Rakoczy, 2003) of both first and second order (Frith, 2007) is thought to be a process in interlocking agents' mutual intentional actions, and thereby carrying out interactions. Indeed neuroimaging studies investigating online social interactions have implicated a cortical region (medial prefrontal cortex, MPFC) that is one of the main nodes of the so-called theory-of-mind network. As other aspects of interactions based on shared intentions, mutual expectations, commitments and obligations (Gilbert, 1992) have been emphasized by other accounts. To illustrate, if I am under the impression that my friend and I are attempting to make Turkish delight together, I expect her to perform her part of the task, such as moving aside when I pour sugar into the boiling water. If she were to suddenly stop what she was doing to leave the kitchen, I would naturally object because she has broken our commitment to make the Turkish delight together. Young children are observed to have acquired such an understanding of normative commitments to social interactions (Graefenhain, Behne, Carpenter & Tomasello, 2009).

The subject of shared intentions has also been a point of conflict for philosophers. In contrast to Bratman's account that focuses on interlocking individual intentions, others have argued for the existence of plural subjects, which might be reflected in the intuitive sense of 'togetherness' commonly identified with shared intentionality. Accordingly, when acting collectively individuals' intentions get organized in such ways that a particular intention profile emerges that resembles that of an individual. This emergent profile, so goes the argument, cannot be accounted for by the individual intentions, and should be attributed to a plural subject that holds a 'we-intention' (Gilbert, 2009; Tollefsen, 2005; Tuomela, 2006).

An open question concerns how we perceive social interactions that are based on shared intentions. If we are inclined to represent the agent of a collaborative action as a single body (e.g. football team), does our processing of mental or affective states associated with the collective behaviour resemble our processing of those associated with an individual behaviour? When we attribute an intention to an interaction, do we attribute a single shared intention or multiple independent intentions? Are processes of action perception modulated by different ascribed intentional relations (i.e. shared intentions or parallel intentions)? These questions are addressed in Chapter 5 of the thesis.

## **Outline of Chapters**

**Chapters 2 and 3** address the question whether motor laws governing action execution constrain action simulation, particularly at a neuronal level. Two studies used Fitts' law, one of the most robust laws in motor performance to further test this hypothesis. Chapter 2 describes a study on a neuropsychological patient with a frontal brain lesion that affects motor areas of the brain. It investigated whether a particular violation of Fitts' law the patient displayed in performance was also present in the patient's judgments of the feasibility of movements observed in others. The study presented in Chapter 3 included an action-perception paradigm in

a functional magnetic resonance imaging (fMRI) experiment conducted with healthy adults. The paradigm specifically aimed to manipulate the motor difficulty of observed actions while controlling for perceptual features. The neural response to specific motor parameters in observed actions was explored.

**Chapter 4** reports a study that investigated whether shared task representations during a joint task would result in diffusion of information across actors during memory encoding. Two individuals performed a task that was distributed between them. They classified words into their individually assigned categories and were later tested for their memory. Two experiments demonstrated that sharing task representations affected formation of memories. Individuals remembered items belonging to their partners despite a lack of incentive to do so. This finding implies that cooperation could as well be a mechanism, among others, that lies on the basis of formation of shared knowledge systems, and opens up new research avenues to be explored.

The study reported in **Chapter 5** compared the perception of multiple individuals' actions that were or were not based on shared intentions. The main question of interest was whether the processing of joint actions involving shared intentions is subserved by different neural computations than the processing of multiple individual actions without shared intentions. Accordingly, in an fMRI study I compared the neural responses to observing perceptually identical actions of multiple individuals that were either driven or not driven by a shared intention.

**Chapter 6** discusses the theoretical implications of the findings presented in Chapters 2-5.



## Chapter 2

You: Does impairment in action execution impair perception of individual actions?

A version of this chapter is published as:

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The role of motor simulation in action perception: A neuropsychological case study.  
*Psychological Research*, 73(4), 477-485.

## **Abstract**

Research on embodied cognition stresses that bodily and motor processes constrain how we perceive others. Regarding action perception the most prominent hypothesis is that observed actions are matched to the observer's own motor representations. Previous findings demonstrate that the motor laws that constrain one's performance also constrain one's perception of others' actions. The present neuropsychological case study asked whether neurological impairments affect a person's performance and action perception in the same way. The results showed that patient DS, who suffers from a frontal brain lesion, not only ignored target size when performing movements but also when asked to judge whether others can perform the same movements. In other words DS showed the same violation of Fitts' law when performing and observing actions. These results further support the assumption of close perception action links and the assumption that these links recruit predictive mechanisms residing in the motor system.

## **Introduction**

The assumption that the motor system supports cognition has gained a lot of popularity in the last decade. It implies that basic bodily and motor processes constrain not only what individuals can perceive, feel, and do, but also how they understand and relate to others (Sommerville & Decety, 2006). One way to conceptualize motor contributions to perception and cognition is the assumption of common coding (Prinz, 1997; Prinz & Hommel, 2002) that is inspired by James (1890) ideomotor principle for voluntary action. This principle states that imagining an action creates a tendency to carry it out. Common coding theory extends the ideomotor principle and claims that the same mental representations are involved in performing actions and observing actions. These representations code the “perceivable” effect of actions. During performance common codes are activated from the inside and then further specified in the motor system. During observation they are activated from the outside and lead to “motor resonance”.

A large body of neurophysiological evidence supports the assumption of a common coding for perception and action (Rizzolatti & Craighero, 2004). Mirror neurons found in the premotor cortex of the monkey brain and the analogous mirror system in humans are engaged in perception as well as in execution of action supporting the view that others’ actions are coded in a functionally equivalent way as one’s own actions. The primary function of the common representations implemented in the mirror system has so far been attributed to action understanding (Rizzolatti & Craighero, 2004), that is, extracting the goals that underlie observed actions (Wohlschlaeger & Bekkering, 2002; Hamilton & Grafton, 2006; 2008; Rizzolatti, Fogassi, & Gallese, 2001). However, there is also reason to believe that mirror matching contributes to predicting others’ actions in real time (Knoblich & Flach, 2001; Knoblich, Seigerschmidt, Flach, & Prinz, 2002; Wilson & Knoblich, 2005). Accordingly, simulation theories (Jeannerod, 2001; Wilson & Knoblich, 2005; Schubotz, 2007) propose that people use internal models (Wolpert, Ghahramani, &



Jordan, 1995; Frith, Blakemore & Wolpert, 2000) to predict the future sensory and perceptual consequences of observed actions. The idea is that the same models that are used to plan one's own actions can be exploited in action perception.

In the context of action planning, internal models reflect previously experienced relationships between actions and their outcomes (Kawato, 1999; Miall, 2003; Wolpert et al., 1995). With every motor command generated during movement execution, the motor system produces an efference copy of that motor command in parallel. Based on this copy, the forward model estimates the sensory consequences of the movement. The estimate stands in for the re-afferent information coming from sensory channels and is used in further processing until the actual re-afferent information arrives at the central nervous system (e.g., Frith, Blakemore & Wolpert, 2000). The critical assumption in the simulation accounts above is that forward models are instrumental in action perception. Accordingly, an observed action is matched with our own repertoire and is simulated via the internal models using the same efference copy. In other words, perception and action matching allows us to exploit already existing predictive mechanisms in the motor system to make sense of others' actions.

In summary, "motor theories" of action perception suggest that perceived actions are matched to one's own action repertoire and that this matching activates internal models that allow one to predict the outcome of perceived actions. One testable implication of these assumptions is that the principles or "laws" that constrain production of movement should affect action perception. The reason is that motor simulations should impose the constraints of one's own motor apparatus onto observed actors. Before describing a neuropsychological case study on patient DS that further tested this claim we shortly summarize earlier evidence that has been obtained with regard to two well-established motor laws: The two-thirds power law (Lacquaniti, Terzuolo, & Viviani, 1983) and Fitts' law (Fitts, 1954). In particular, we will focus on results suggesting that these motor laws affect how we perceive others.

### Two-thirds power law

The two-thirds power law (Lacquaniti et al., 1983; Viviani, 2002) describes the relationship between the velocity of a movement and the curvature of its trajectory. The law states that as curvature increases one needs to systematically slow down. As the curvature decreases, on the other hand, one can systematically accelerate the movement. This change in velocity is directly proportional to the change in curvature. The two-thirds power law has been shown to hold for most types of human movement, including manual (Viviani & Mounoud, 1990) or eye tracking movements (de Sperati & Viviani, 1997). Studies that investigated perceptual judgments for movements indicate that the two-thirds power law constrains perception of action in the same way as it constrains production. For example, it was shown that people's perception of geometric and kinematic properties of end-point trajectories, such as drawing and writing (Viviani & Stucchi, 1989, 1992), is systematically biased towards complying with the two-thirds power law (Lacquaniti et al., 1983).

Further support comes from a recent functional MRI study which investigated the neural correlates of the two-thirds power law by presenting participants visual stimuli that were either in compliance with or in violation of this law (Dayan, Casile, Levit-Binnun, Giese & Hendler et al., 2007). The authors found that the stimuli obeying the two-thirds power law yielded stronger and more widespread activation in areas associated with action production, action perception and visual motion processing.

Kandel, Orliaguet and Boe (2000) investigated whether the two-thirds power law also influences an observer's ability to predict the future course of handwriting trajectories. They found that the predictions were most accurate for trajectories that complied with the law and became less accurate as trajectories were manipulated to deviate from it. Flach, Knoblich and Prinz (2004) reported similar findings for a representational momentum paradigm (Hubbard, 2005), where subjects are typically asked to predict the future course of a movement. Errors in prediction

were smaller when the observed movement trajectories complied with the two-thirds power law.

The results described above suggest that anticipating the future course of a perceived movement is easier when it corresponds to the constraints that govern the actions that produce this movement. They can be interpreted as support for the claim that we perceive and understand movements through the lens of our motor repertoires. When perceived events are predictable by an internal model in the motor system people can better anticipate what will follow than when the perceived events are not predictable by an internal model.

#### Fitts' law

Fitts' law (Fitts, 1954) is perhaps the most stable law in human motor control (for a review, see Plamondon & Alimi, 1997), and has been studied extensively by the human computer interaction (HCI) field as well as psychophysics. The law captures the speed accuracy trade-off observed in human movement, and states that the average time it takes to move between two targets is determined by the width of the targets and the distance separating them. With increasing target width, one can move faster between the targets without missing them. With increasing distance between targets, one takes longer to move between them. Fitts' law expresses this trade-off between speed and accuracy as:  $MT = a + b \times ID$ ; where MT is movement time, ID is the index of difficulty, and a and b are empirical constants. The critical variable is the ID, which relates the amplitude (A) of the movement to the width (W) of the targets. It is expressed as:  $ID = \log_2 (2A/W)$ .

The main quantitative prediction that can be derived from Fitts' law is that different combinations of target width and movement amplitude can yield the same index of difficulty, and thus the same MT (Table 2.1). Fitts' law holds for many forms of movement production including different effectors and movement contexts, with only a few exceptions (e.g., Chi & Lin, 1997; Danion, Duarte, & Grosjean, 1999).

Decety and Jeannerod (1995) were the first to demonstrate that Fitts' law not only

holds for movements that are actually performed but also for movements one imagines to perform. They asked participants to imagine walking in a three-dimensional virtual environment towards gates of varying widths situated at varying distances and found that the mental MT it took the participants to move between the two gates was a linear function of the index of difficulty (ID), just as predicted by Fitts' law. The imagined MT increased with increasing apparent distance between the gates, and with decreasing gate width. This result shows that imagined actions maintain the temporal characteristics of the same actions executed (Decety, Jeannerod, & Prablanc, 1989; Sirigu, Duhamel, Cohen, Pillon & Du Bois et al., 1996, Sirigu, Cohen, Duhamel, Pillon & Du Bois et al., 1995), indicating that the same internal models are at work when performing and imagining actions.

**Table 2.1:** Movement amplitudes used in the experiment as a function of the target width (in cm) and index of difficulty.

Target Width	Index of Difficulty		
	2	3	4
2	4 cm	8 cm	16 cm
4	8 cm	16 cm	32 cm
8	16 cm	32 cm	64 cm

There is also evidence that a person has implicit knowledge of Fitts' law when preparing for future movements, when perceiving the constraints of planned movements, and when evaluating the difficulty of planned movements (Augustyn & Rosenbaum, 2005; Sirigu et al., 1995, 1996; Maruff & Velakoulis, 2000; Slifkin & Grilli, 2006). Other motor imagery studies using a variety of tasks, such as walking (Bakker, de Lange, Stevens, Toni, & Bloem, 2007; Decety & Michel, 1989), simple hand actions (Sirigu et al., 1996; Choudhury, Charman, Bird, & Blakemore, 2007),

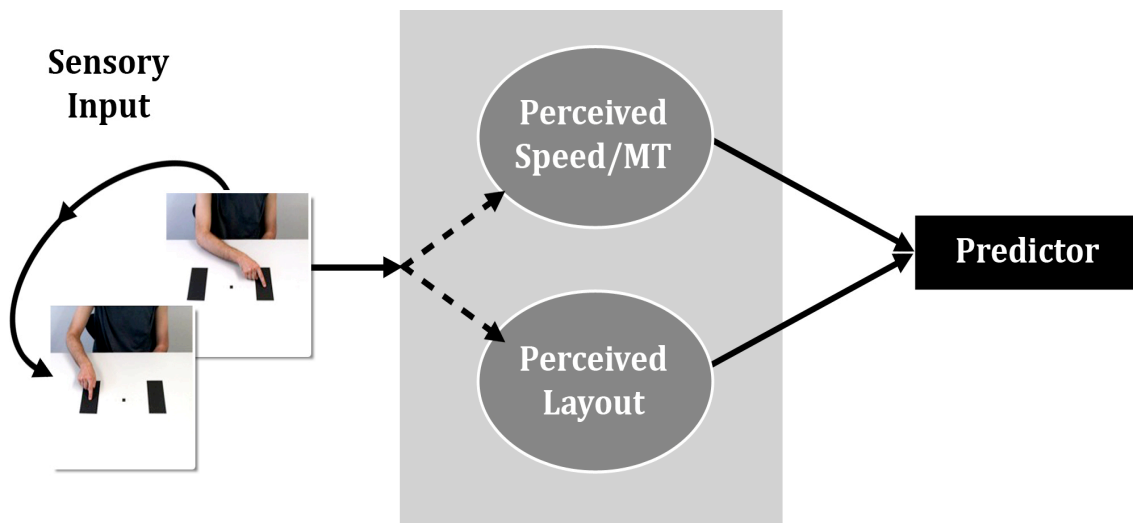
drawing (Decety & Michel, 1989) or reaching targets (Maruff & Velakoulis, 2000) confirm that the same motor representations govern an action whether it is real or imagined. Index of difficulty affects actions in the same way irrespective of their modalities. Taken together, similarity in temporal properties between real and imagined movements (Decety & Jeannerod & Prablanc, 1989; Decety & Michel, 1989) suggests that overlapping motor mechanisms are recruited for both types of movement.

Results from another recent study suggest that observation of action may recruit similar motor processes as performing and imagining movements. In particular, Grosjean, Shiffrar and Knoblich (2007) have shown that Fitts' law holds when people are asked to judge how fast another person can move. In this experiment, participants were shown alternating pictures of a person moving their arm between two targets. Index of difficulty (ID) was varied choosing appropriate movement amplitudes and target widths. Nine different amplitude/width combinations were used, yielding three conditions for each of three IDs. The participants were asked to report whether the person could perform such a movement without missing the targets. Alternating pictures were chosen instead of video clips to avoid any additional information provided by movement trajectories. The perceived MTs were defined in terms of the speed at which the participants reported an equal number of 'possible' and 'impossible' judgments.

The perceived MTs were found to vary linearly as a function of ID ( $r^2 = 0.96$ ), indicating that the MTs did not vary as a function of target width or movement amplitude alone. These results demonstrated that the same motor law constraining action production and motor imagery constrains action perception as well. Providing a solid support for motor contributions to action perception, this study reinforced the relationship between action production, motor imagery and action perception, in line with evidence for overlapping neural systems for these three motor domains (Grezes & Decety, 2001; Rizzolatti & Craighero, 2004).

The authors explain these results with the following model (see Figure 2.1)

postulating that simulations are run via two separate routes. One route deals with the contextual information surrounding an action (task layout) and one deals with the kinematics (spatiotemporal characteristics) of the observed action. A representation of the task layout constrains internal models towards simulating the action so that it could be executed in that given environment (cf. Pacherie, 2008). In other words, predicted speed (or MT) for the movement depends on the context within which the action is embedded and the biomechanical constraints reflected in the internal models. In order to decide whether an observed movement is doable or not, the speed prediction is contrasted with the perceived movement speed.



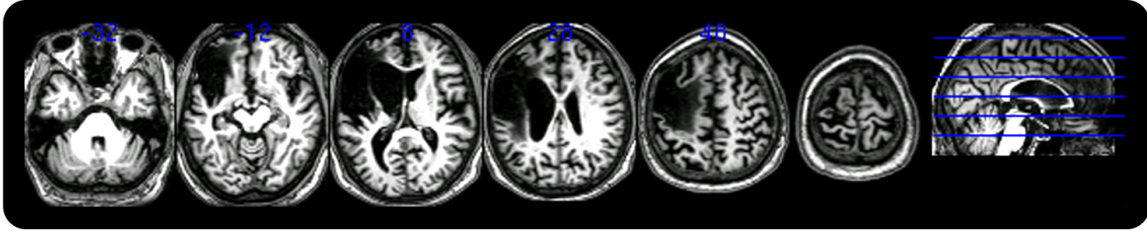
**Figure 2.1:** Proposed dual route model of action perception. Contextual information and the kinematics of the observed actions are coded independently via separate routes of internal simulations, The two routes feed into and are reconciled by the predictors that yield a judgment with respect to the ‘doability’ of the perceived action.

The dynamic model of Erlhagen, Mukovskiy, & Bicho (2006) suggests possible neural correlates of these separate routes. In this model, simulation and action understanding are integrated within a continuous dynamic process. Accordingly, contextual information, movement information, and the goal of the movement are represented as dynamic activity in layered neural networks. One part of the model consists of the premotor-parietal-STS (superior temporal sulcus) mirror circuitry responsible for action observation and action execution. This circuitry is interconnected with a layer in prefrontal cortex (PFC) that is proposed to encode the intentional action goal framed by the context in which the action is set.

If the contextual constraints in which actions are embedded are processed by prefrontal areas, as claimed by Erlhagen and colleagues (2006), then we would expect a lesion in this area to misrepresent the context of an action, and hence the reasons driving it. Particularly in a Fitts' task, a patient with a prefrontal lesion would not be able to integrate the task layout into his representation of the observed movement. This, in turn, would not only impair his ability to adapt his movement speed but in the same manner his ability to judge whether an observed person can achieve a certain movement speed or not. In the following, we report a study that tested this hypothesis in the neuropsychological patient DS whose lesion encompasses the left frontal lobe.

### Patient DS

DS is a 74-year-old former train inspector who suffered a stroke in 1995. He is able to function at a relatively self-sufficient manner despite his hemiplegia of the right side. Following his accident, a wide range of neuropsychological measures and an MRI-scan of his lesion were obtained. His MRI-scan revealed damage to the left inferior, middle and superior frontal gyri (Figure 2.2). DS's scores on low level visual perception and object naming were relatively normal. He scored 100% on unusual views matching, and 86% on naming everyday objects. Despite a few semantic errors in naming, DS used these objects appropriately.



**Figure 2.2:** MRI scans of patient DS. He suffers from lesions in left inferior middle and superior frontal gyri due to a stroke.

## Method

### Participants

In addition to patient DS, five healthy control participants were tested in exchange for course credit or money. The control participants reported normal or corrected-to-normal vision. They were not age-matched as Fitts' law has been shown to hold across different age groups (Skoura, Papaxanthis, Vinter, & Pozzo, 2005).

### Materials

Stimulus presentation and response registration were managed by an IBM compatible computer using E-Prime software version 1.0 (Psychology Software Tools, Inc.). The stimuli used were pairs of digital photographs of an arm pointing at one of the two targets placed on a flat surface (Figure 2.3). The two targets were of identical widths and were separated by varying amplitudes. Across trials, each of three widths (2, 4 and 8 cm) was combined with three of five amplitudes (4, 8, 16, 32 and 64 cm) to make up for three IDs (2, 3 and 4; Table 2.1). The pair of photographs was repeatedly alternated to create apparent motion.

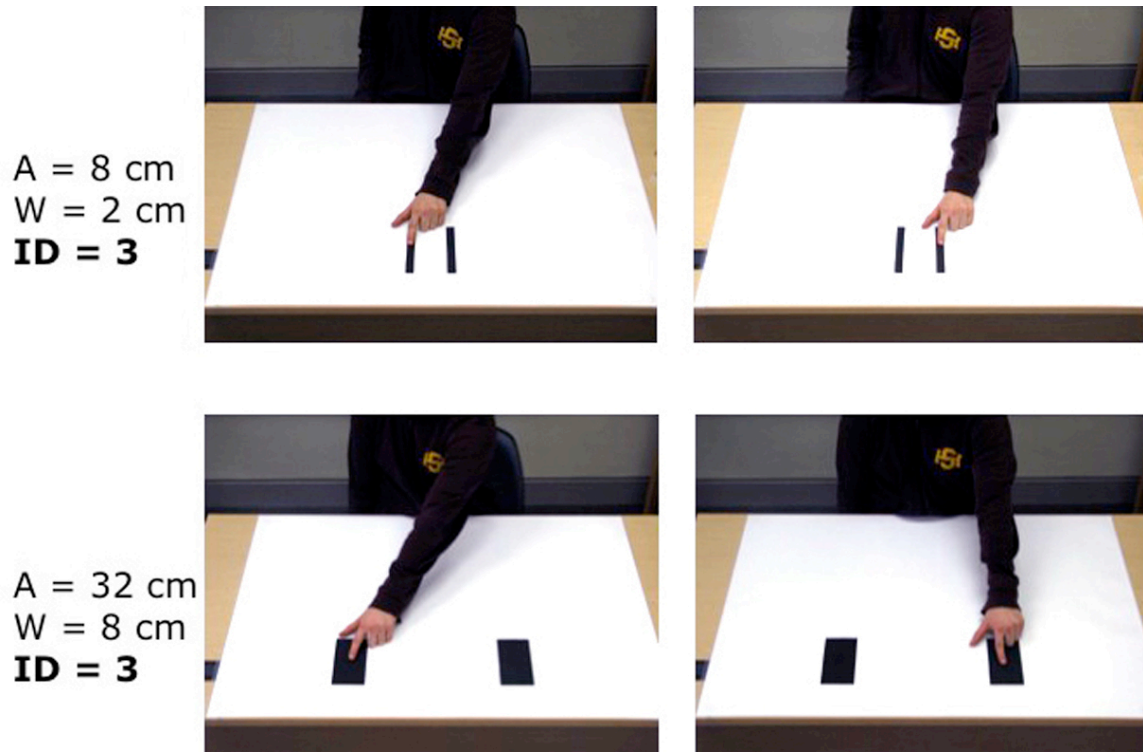
### Procedure and design

The rate at which the stimuli were alternated was set at 1 of 11 stimulus-onset asynchronies (SOAs), which also corresponded to the durations of individual



frames. SOAs ranged from 150 to 650 ms in increments of 50 ms. Each trial started at an SOA of either 150 or 650 ms. The SOAs could be changed with key presses. Key (1) shortened the SOA by one step, key (2) lengthened the SOA by one step, and key (3) was programmed to go on to the next trial. The task was to choose the speed at which the movement between the two targets was just doable. The participants could modify the SOAs as often as they wanted until they were satisfied, before they moved on to the next trial. The SOA that was ultimately chosen on a given trial was defined as the MT that was perceived as just doable. A 3 (width) x 3 (ID) x 2 (hand) factorial design was used. Half of the stimuli showed right-hand movements and half showed left-hand movements. Each block of 72 trials was presented to the participants in a random order, following a short practice session. The running time for each block was roughly 20 min and three blocks were completed.

The patient was also asked to execute the same actions presented in the action perception task. Targets of same widths as in the previous task were placed across each other at varying amplitudes, to create the same IDs (Table 2.1). DS was instructed to move between the targets as fast and as accurately as possible while a video camera recorded his performance. Produced MT for a given trial was defined as the average duration of a single movement between the targets, i.e., 10 s divided by the total number of performed movements. The patient could perform the task with his left hand only, due to his hemiplegia. Each of the nine trial types was tested twice. Trials were presented in a random order within the same block. No control participants were tested for this task, as Fitts' law is well established in action production across age groups (Skoura et al., 2005).



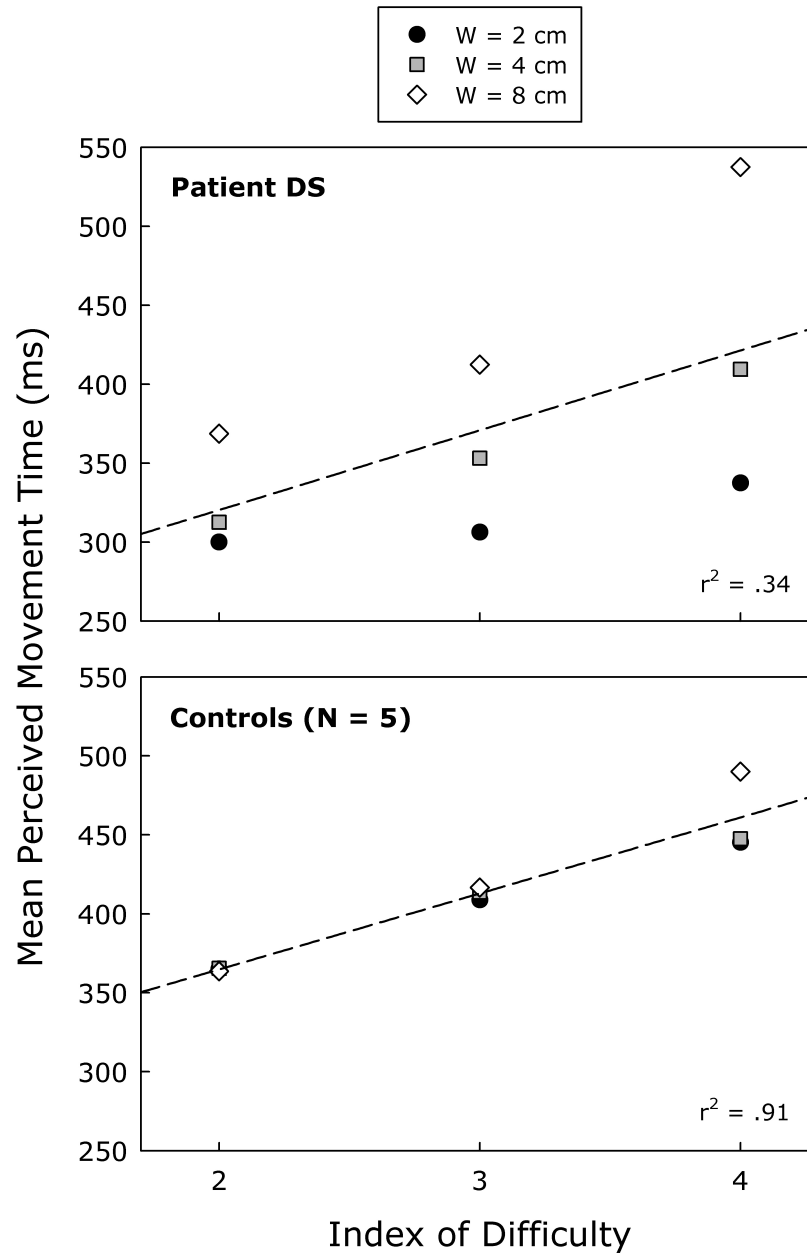
**Figure 2.3:** Sample stimuli with different combinations of target width (W) and movement amplitude (A) leading to the same index of difficulty (ID).

## Results

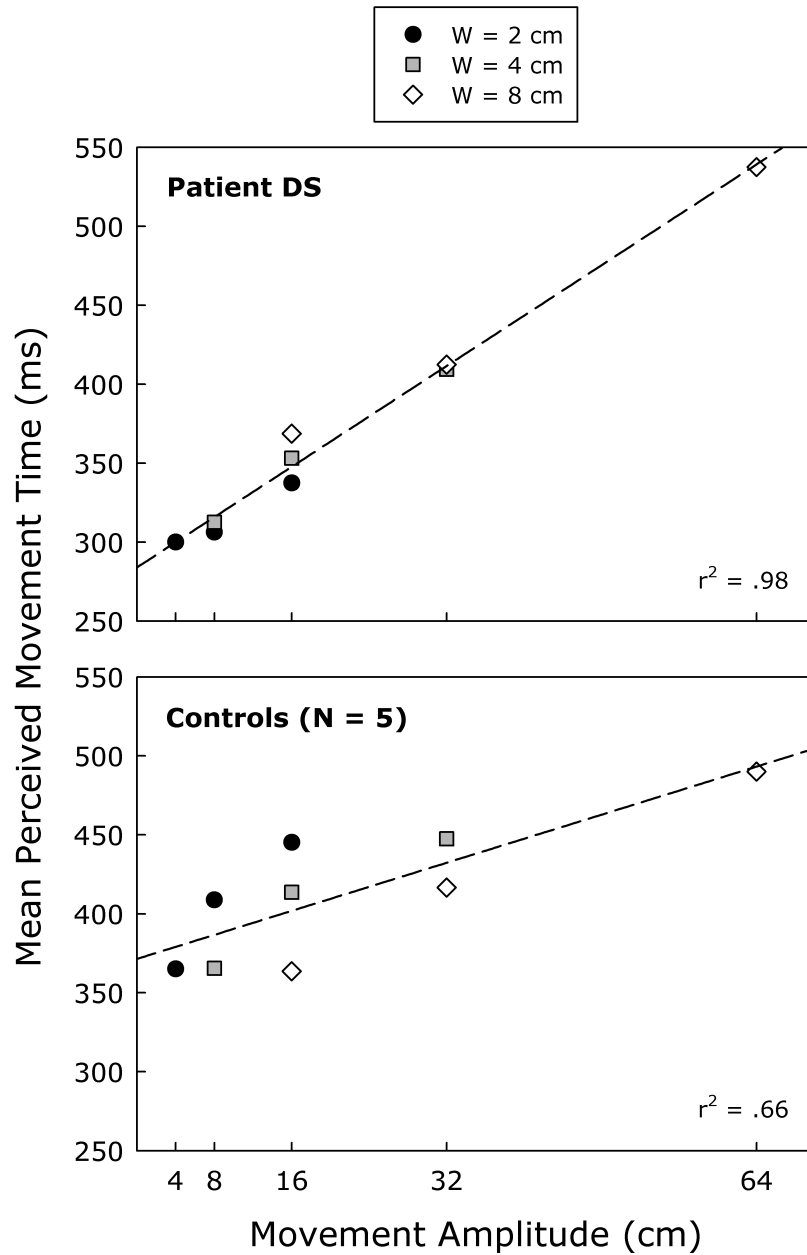
Figure 2.4 presents the mean perceived MTs as a function of width and index of difficulty (ID), for patient DS and the five control participants. The results for the controls are consistent with Fitts' law and our previous findings (Grosjean et al., 2007). Perceived MTs increased linearly with ID (see bottom panel of Figure 2.4). The regression analysis yielded a significant  $r^2$  of 0.91 ( $F(1, 7) = 74.13, p < 0.001$ ) and the following regression equation for MT:  $MT = 269 + 48ID$ . In contrast, the data for patient DS did not obey Fitts' law (see top panel of Figure 2.4). ID only accounted for a small and non-significant portion of the variance in DS's perceptual judgments ( $r^2$

= 0.34,  $F(1, 7) = 3.61$ ,  $p = 0.099$ ). The resulting regression equation was  $MT = 219 + 51ID$ . Figure 2.5 displays the same data plotted as a function of movement amplitude (A), that is, distance between the targets instead of ID. As can be seen in the top panel of the figure, movement amplitude was an almost perfect predictor for which MTs DS perceived as just doable, as evidenced by the  $r^2$  of 0.98 ( $F(1, 7) = 451.93$ ,  $p < 0.001$ ). The resulting regression equation was  $MT = 284 + 4A$ . As would be expected, based on the results presented above, movement amplitude was a weaker predictor for the control participants' performance (see bottom panel of Figure 2.5) because it fails to take into account the influence of W ( $r^2 = 0.66$ ,  $F(1, 7) = 13.83$ ,  $p < 0.01$ ). The resulting regression equation was  $MT = 371 + 2A$ ).

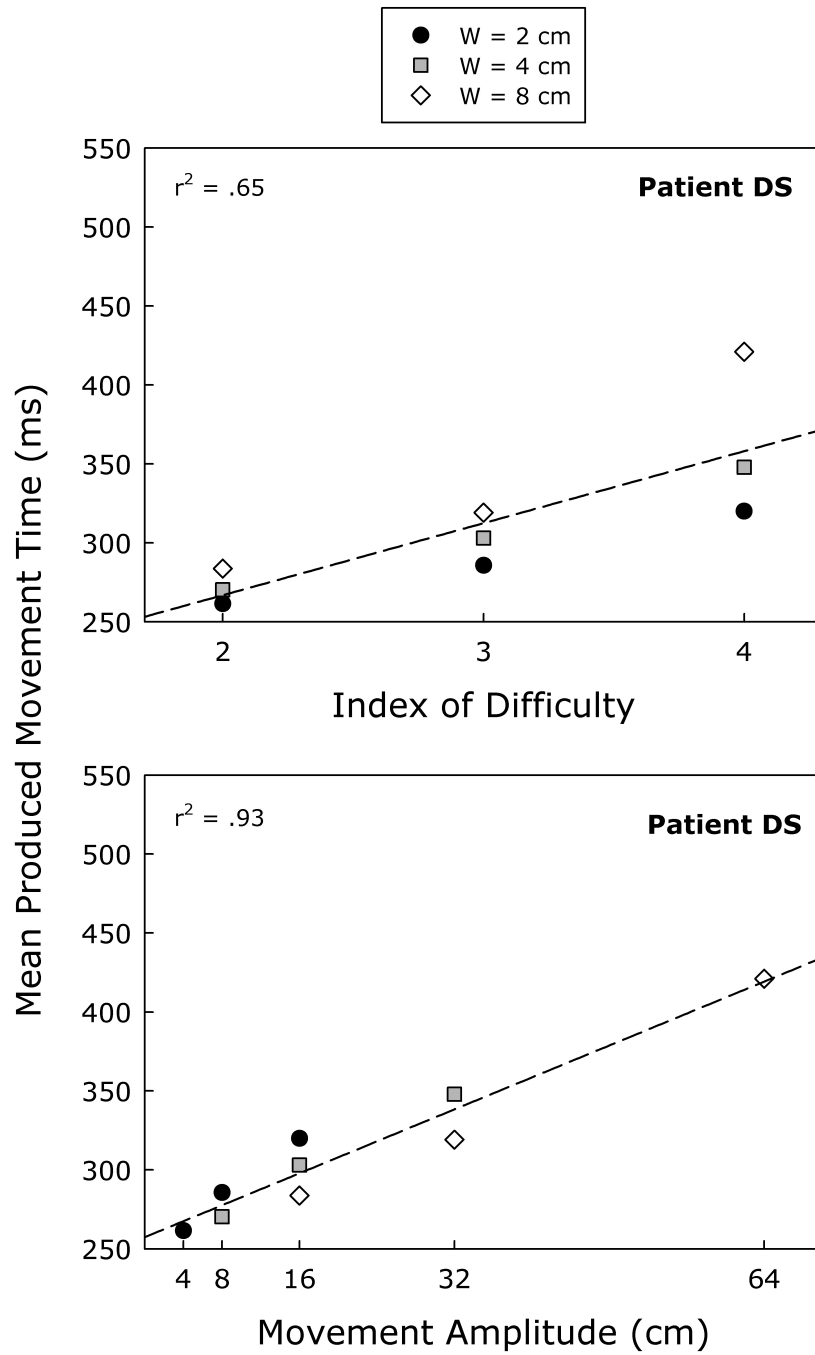
The action production data gathered from DS are depicted in Figure 2.6. As was already observed for his perceptual data, movement amplitude ( $r^2 = 0.93$ ,  $F(1, 7) = 93.44$ ,  $p < 0.001$ , regression equation  $MT = 257 + 3A$ ; see bottom panel of Figure 2.6) proved to be a much better predictor of his performance than ID ( $r^2 = 0.65$ ,  $F(1, 7) = 13.03$ ,  $p < 0.01$ , regression equation  $MT = 176 + 46ID$ ; see top panel of Figure 2.6). Thus, both his perceptual and production data violated Fitts' law in similar ways: MT was linearly related to movement amplitude rather than index of difficulty. Finally, in line with what would be expected if DS relied on a similar set of representations and/or processes in both tasks, we found that his perceived and produced MTs were almost perfectly correlated across conditions ( $r^2 = 0.88$ ,  $F(1, 7) = 50.34$ ,  $p < 0.001$ ).



**Figure 2.4:** Mean perceived movement time as a function of target width (W) and index of difficulty for patient DS (top panel) and the control participants (bottom panel). The corresponding linear regression lines and coefficients of determination are also provided



**Figure 2.5:** Mean perceived movement time as a function of target width (W) and movement amplitude for patient DS (top panel) and the control participants (bottom panel). The corresponding linear regression lines and coefficients of determination are also provided.



**Figure 2.6:** Mean produced movement time as a function of target width (W) and index of difficulty (top panel) and movement amplitude (bottom panel) for patient DS. The corresponding linear regression lines and coefficients of determination are also provided.

## Discussion

The results clearly indicate that patient DS relies solely on movement amplitude (the distance between two targets) when judging whether a movement was doable or not, and disregarded the target width. This suggests that DS seems to have lost the ability to integrate contextual constraints in action simulations, resulting in a deficiency in predicting an appropriate action speed for that given environment. Consequently, the resulting speed prediction was solely based on the amplitude of the movement. At the same time, the performance data indicated exactly the same deficit when he was asked to move as quickly as possible between the two targets. This suggests that DS's lesion affects his performance and his perception of others' movements in the same way.

Although the control participants used in our study were not age-matched, it is unlikely that DS's results can be attributed to general motor deterioration due to aging. First, Skoura et al. (2005) demonstrated that Fitts' law holds for motor production in the elderly. Potentially troubling is their finding that elderly participants disregarded varying target widths during the motor imagery task (but not the motor production task). This finding seems to converge with the present result that patient DS disregarded width. It has to be kept in mind, however, that index of difficulty accounts for a much lesser amount of variance in DS's doability judgments for perceived movements, than it accounted for in the motor imagery condition ( $r^2 = 0.34$  and  $0.89$ , respectively) in Skoura et al.'s study on elderly participants. These numbers seem to rule out the possibility that patient DS's selective impairment is merely a by-product of aging.

It should also be noted that Skoura and colleagues attribute the violation of Fitts' law in imagined movements to the aging parietal cortex. Sirigu et al. (1996) similarly found that patients with parietal lesions violated Fitts' law in the same domain (motor imagery). The possibility has to be acknowledged that patient DS's diffuse lesion in the frontal lobe might encompass this area's links with the adjacent parietal lobe and result in his selective disregard to the target widths. Importantly,

however, both mentioned studies found that parietal impairment did not yield to violation of Fitts' law in action production, but only in motor imagery. In contrast, patient DS violated Fitts' law in both of the tested action domains. Therefore, his parallel impairment in action production and action perception cannot be attributed to a potential injury in his parietal cortex.

The dynamic model outlined by Erlhagen and colleagues (2006) provides a plausible explanation to patient DS's data. In this model the mirror circuitry (i.e. superior temporal sulcus, inferior parietal lobule and the inferior frontal gyrus) performs the matching of observed actions with the existing motor repertoire. The PFC, on the other hand, acts as the 'goal layer' (ibid. p. 177) and encodes the goal of the observed action, which is constrained by the action context. In DS's case, the PFC cannot perform this function and the matching process between perception and action proceeds orthogonally to the action context.

## **Conclusions**

The results of the present study clearly indicate that DS' data are best understood as reflecting a specific deficit that is caused by a brain lesion that affect action production and action perception in exactly the same way. When presented with a Fitts' like task, DS's 'doability' judgments for observed movements were found to be a direct function of the distance between targets. Remarkably, DS's produced movements slowed down as this distance increased, indicating that in both cases patient DS exhibited a specific disability to integrate target size into his motor representation. As stipulated by Fitts' law, previous research in healthy adults has demonstrated that difficulty of a movement (reflected in MT) is a function of the target width and the distance between the target pair. In line with the dynamic model proposed by Erlhagen, we attribute this specific deficit in DS to his lesion of the prefrontal lobe that precludes influences of the task layout on motor simulation. Although DS still perceives others' action capabilities through the lens of his own motor repertoire, the brain systems encoding task context are dysfunctional and can therefore not inform the simulations. This is not to say that all influences on motor



simulations are top-down. Previous research has shown that the lack of peripheral (bottom-up) input to the body schema can also lead to difficulties in action observation and action understanding (Bosbach, Cole, Prinz, & Knoblich, 2005; Bosbach, Knoblich, Reed, Cole, & Prinz, 2006).

Patient DS is yet another illustration of how mechanisms governing action performance constrain what is perceived to be 'doable' in others. In functional terms this suggests a common coding of perception and action that allows perceived actions to be matched to one's own action capabilities (Prinz, 1997). Once common codes are activated the motor system runs simulations to predict the likely future of the ongoing actions that are being observed, thereby directly serving perception. The use of such simulations, which are evidently contingent upon the observer's motor repertoire, renders perception a function of motor processes.

Simulations in general can be defined as partial recreations of previously experienced perceptual as well as motor states (Barsalou, 2008). They serve as the means through which we anticipate the world around us thereby allowing for further mental processing. This emphasizes the neglected flipside of the bidirectional link between bodily and mental states and offers us a plausible explanation as to how our interactions with the world ground cognition.

## Chapter 3

You: Do the motor specific parameters of an observed action engage the motor system?

A version of this chapter is published as:

Eskenazi, T., Rotshtein, P., Grosjean, M. & Knoblich, G. (2011). The neural correlates of Fitts' law in action observation: An fMRI study. *Social Neuroscience*, 7(1), 30–41.

## **Abstract**

Previous neuroimaging studies support the assumption of a strong link between perception and action, demonstrating that the motor system is involved when others' actions are observed. One question that is still open to debate is which aspects of observed actions engage the motor system. The present study tested whether motor activation corresponds to the difficulty of the observed action, using Fitts' law. This law postulates that the difficulty of any movement (ID) is a function of the distance to the target (A) and the target width (W). In an observation task, the ID of the observed action was manipulated orthogonally to W (by using five different As). The results revealed activity in the primary motor cortex, the supplementary motor area, and the basal ganglia in response to increasing ID levels, but not in response to different levels of A or W. Thus, activation in the motor system during action observation is not driven by perceptual parameters but by the motor difficulty of the observed action.

## Introduction

Numerous studies have shown that the motor system participates in action observation (e.g., Calvo-Merino et al., 2006; Grèzes & Decety, 2001; Hamilton & Grafton, 2006; 2008; Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010). For instance, it is known that people can acquire new motor skills through observation (Cross, Kraemer, Hamilton, Kelley & Grafton, 2009; Mattar & Gribble, 2005) or mental imagery that entails mentally rehearsing actions (Olsson, Jonsson, Larsson, & Nyberg, 2008). Furthermore, acquiring new motor skills influences the way people observe others' actions that require the same skills (Aglioti et al., 2008). Similarly, behavioural studies on motor laws, such as Fitts' law (Fitts, 1954), suggest that motor laws constrain action production and action simulation in the same way (Grosjean et al. 2007; Decety & Jeannerod, 1995). In particular, both the speed with which an action can be performed and the speed at which an action is perceived as being just doable are governed by the index of difficulty as formulated by Fitts' law. Thus, the same speed– accuracy trade-off observed in human performance dictates people's judgments about what is doable for others.

Briefly, Fitts' law parameterizes this trade-off characterizing biological motion. Accordingly, the average movement time (MT) to reach a target is defined as a linear function of index of difficulty (ID) of the movement:  $MT = (a+b) \times ID$ . ID in turn is a function of the distance to be covered, commonly referred to as amplitude (A) and the width (W) of the target to be reached:  $ID = \log_2(2A/W)$ . The longer the distance to the target, the more difficult the action becomes. By the same token, increasing target width reduces the accuracy requirement of the action and thus the index of difficulty. Fitts' law holds for most performed actions (with the notable exception of saccadic eye movements—Chi & Lin, 1997; see also Danion, Duarte, & Grosjean, 1999), as well as imagined (Decety & Jeannerod, 1995) and perceived actions (Eskenazi, Grosjean, Humphreys, & Knoblich, 2009; Grosjean et al., 2007).

The study conducted by Grosjean and colleagues (2007) presented participants with alternating pictures of a person moving an arm between two identical targets, and they were asked to judge whether an average person could perform the observed movement at this speed. ID was systematically varied, choosing appropriate target widths and movement amplitudes. In other words, motor difficulty was varied so that it could not be derived from perceptual information about movement amplitude or target size alone. Rather, it reflected the difficulty of performing the observed movement. The results clearly showed that ID was an excellent predictor of the participants' "doability" judgments, providing strong support for the notion that motor constraints can influence perception (Grosjean et al., 2007).

The above findings provide evidence that motor simulations (Jeannerod, 2001; Wilson & Knoblich, 2005) are a key mechanism through which the motor system contributes to observation of actions. Motor simulation, in the context of action perception, refers to applying internal models that are used in planning and execution of one's own actions to perceived actions. Evidence for the involvement of motor-related brain regions during action perception is further provided by numerous neuroimaging studies (for a recent review, see Rizzolatti & Sinigaglia, 2010). Neural areas famously comprising the human mirror system, also known as the action observation network (AON) (Grafton, 2009), include the bilateral superior temporal sulcus (STS), the inferior parietal lobule (IPL), the inferior frontal gyrus (IFG), and the premotor cortex (PM). Other neural regions outside this mirroring network contributing to motor production, such as the supplementary motor area (SMA) (Dayan et al., 2007; Nachev, Kennard & Hussain, 2008), the basal ganglia (BG) and cerebellum (Blakemore, Frith, & Wolpert, 2001; Wolpert, Miall, & Kawato, 1998), and, importantly, the primary motor cortex (M1) (Caetano, Jouki, & Hari, 2007; Kilner & Frith, 2007; Kilner, Marchant, & Frith, 2009), have also been implicated in action simulation.

The mirroring system in humans is thought to support action understanding by recognizing actions in terms of their general aspects, particularly their object-related goals (cf. Rizzolatti & Sinigaglia, 2010), or the intentions delineated by the context in which the action is embedded (Iacoboni, 2005). This has been further elaborated by other theories of action perception. For example, it is argued that recognition is realized at several levels of visual-motor hierarchy in the human brain, each of which is encoded by a different node of the action observation network (Grafton, 2009; Grafton & Hamilton, 2007). These levels include the long-term goal or the intention level, the goal level, and the muscle/kinematic level of action representation. The short-term, object-related goal of an action is encoded in the anterior IPL, whereas the kinematics of primarily grasping actions is represented in the IFG node, an area hypothesized to support representation of produced movements.

There is also evidence that motor simulation taps into more specific parameters of observed movement as well, such as effort, speed (Aglioti et al., 2008), force (Slifkin, 2008; Wolpert & Flanagan, 2001), or internal states derived from the kinematics (Bosbach, Cole, Prinz, & Knoblich, 2005). Studies of peripheral activity during observation of effortful actions provide a similar picture. Increase in autonomic responses such as respiration and heart rate are reported during simulation of (Mulder, de Vries, & Zijlstra, 2005) as well as observation of effortful tasks (Decety, Jeannerod, Durozard, & Baverel, 1993). It has also been shown that participants have an accurate judgment of task difficulty prior to execution. This finding clearly suggests that motor simulation is the mechanism through which a judgment is reached (Frak, Paulignan, & Jeannerod, 2001). Witt, Proffitt, and Epstein (2005) demonstrated that people perceive the effort involved in an anticipated task in terms of their action capabilities. Of particular interest, perceived difficulty at a Fitts' task has been shown to correlate with the actual index of difficulty of the task (Delignières, 1998).

It is unknown whether or how the motor-related brain areas are involved in

simulating the specifics of an action, particularly the difficulty as formulated by Fitts' law (Fitts, 1954). To investigate this question, we conducted a functional magnetic resonance imaging (fMRI) study of action observation, with a paradigm similar to the one described in Grosjean et al. (2007). In this paradigm, participants were asked to judge the “doability” of perceived actions. In the present study, participants viewed a pointing human hand alternately moving between two targets of identical size. Three different levels of ID were obtained with different combinations of target width (W) and distance (A). In accordance with the simulation account, we predicted increasing activity in motor areas with increasing levels of ID. We hypothesized that observed ID, which is a function of these two variables, but not object information (i.e., target width) or the contextual setup of the observed movement (i.e., distance between targets, movement amplitude), would activate the motor system of the observer. We did not expect to find a similar motor activation in a control condition, in which a pen instead of a pointing hand moved between the two targets (Figure 3.1). We predicted that, despite the perceptual similarity between hand and object stimuli, the motor system would be activated only during human movement and not during object movement.

## Method

### Participants

Ten right-handed participants (age range 20–29 years, six women) were paid to take part in the experiment. All gave their informed consent and were naive to the purpose of the experiment. None had a history of any neurological or psychiatric disorders, and their vision was normal or corrected-to-normal. Data from one participant were excluded from analysis due to an incidental lesion discovered in his right hemisphere. He was referred to a medical professional. The study was approved by the local ethics committee.

### Behavioural task

*Stimuli and procedure.* Prior to the scanning session, participants were asked to

perform the behavioural task described in Grosjean et al. (2007). In this apparent motion paradigm, participants were presented with alternating still frames of a pointing finger that moved at various speeds between two rectangular targets. The task was to judge whether the person could perform the movement at the observed speed without missing the targets. Pairs of photographs depicted a right index finger touching one of two targets. Targets in each frame were of identical width ( $W$ ) and were separated by a given distance ( $A$ ). Three ID levels (2, 3, and 4) were factorially crossed with three  $W$  levels (2, 4, and 8 cm), resulting in five  $As$  (Table 3.1). The frames were alternated at varying rates—stimulus-onset asynchrony (SOA)—that ranged from 120 to 720 ms with 40 ms increments. The experiment consisted of three blocks, with 144 trials randomly presented in each block. A MacBook Pro Macintosh computer running PsyScope (Cohen, MacWhinney, Flatt, & Provost, 1993) was used for stimulus presentation and response collection.

**Table 3.1:** Movement amplitudes used in the experiment as a function of the target width (in cm) and index of difficulty.

Target Width	Index of Difficulty		
	2	3	4
2	4 cm	8 cm	16 cm
4	8 cm	16 cm	32 cm
8	16 cm	32 cm	64 cm

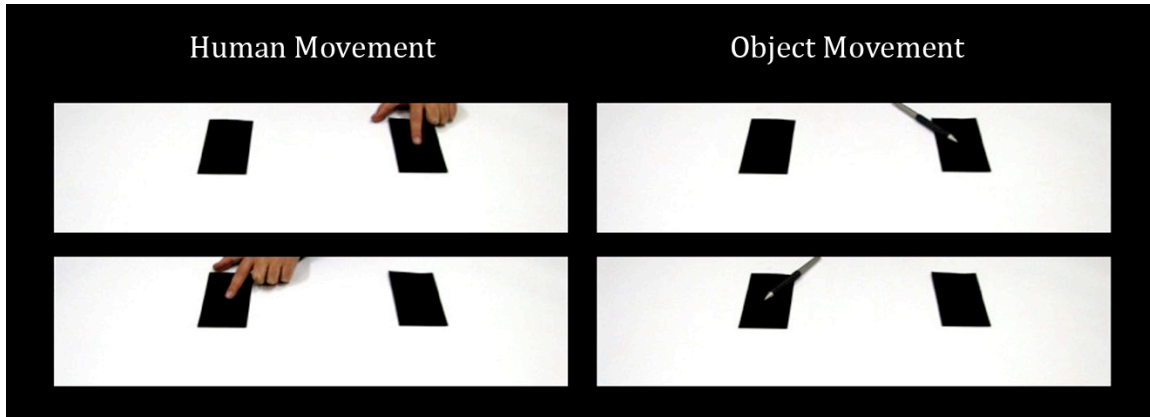
*Data analysis.* For each participant, the proportion of “possible” judgments was computed for each of 144  $W \times ID \times SOA$  combinations. Then, for each of the 9  $W \times ID$  combinations, the perceived MT was defined as the SOA at which the participants gave an equal proportion of possible and impossible judgments (for details concerning this analysis, see supplementary materials). To test whether the data



obeyed Fitts' law, linear regression analyses on the perceived MTs were performed with either ID or movement amplitude as the predictor variable. The analyses were carried out with MATLAB (The Math Works Inc, MU Guide Inc., Natick, MA, 1998).

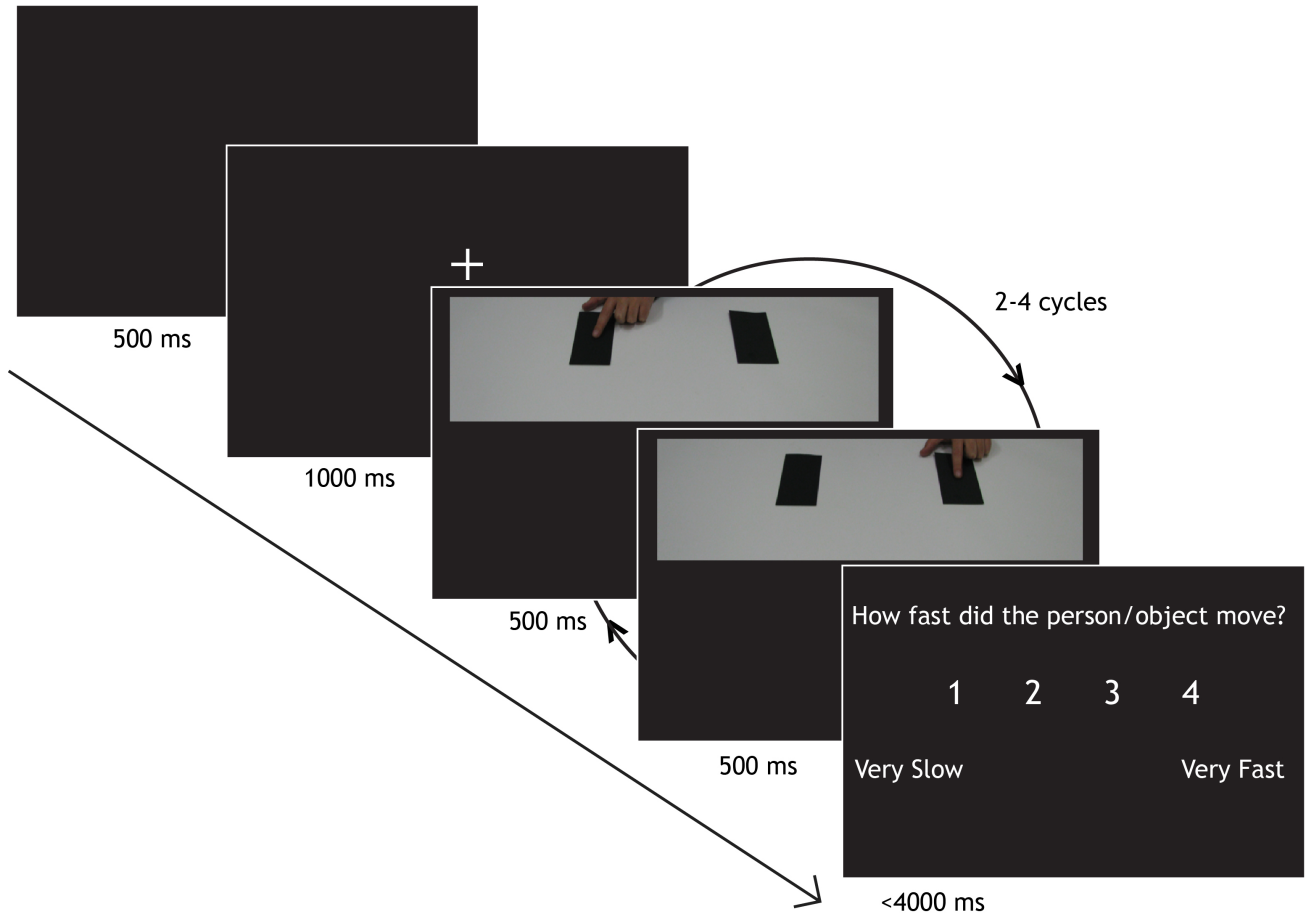
#### fMRI task

*Stimuli and procedure.* A similar apparent motion paradigm was used in the task performed during fMRI data acquisition, albeit with a new set of stimuli. The participants observed a hand moving between two targets. In 20% of the trials, the participants were asked to provide a speed rating of the movement. As in the behavioural task, each of the photograph pairs depicted a finger or a pen (Figure 3.1) pointing at one of the two identical rectangular targets. Here, we included photographs of left and right hands, in order to control for laterality effects in the brain activity. The three levels of ID were set against three levels of W, yielding nine different combinations (Table 3.1). In contrast to the behavioural task, the SOA, that is, the rate at which the still frames alternated, was constant across trials. This was done to control for a potential SOA confound on the ID manipulation. Therefore, any differences in perceived speed would be solely a product of the varying target widths and the distance between them. For example, a sequence with a 500-ms SOA and a low ID may be perceived as a very slow movement, whereas the same sequence with a high ID may be perceived as a faster but still doable movement. As a control, we included an object-movement condition in which a pen, instead of a human finger, appeared to jump between the same targets, separated by the same distances. In order to minimize the perceptual differences between the two conditions, photographs were cropped to include only the hand, without the arm, in the human-movement condition. The object-movement condition presented the pen at an angle to the targets similar to that of the hand in the human-movement condition. It should be noted that this paradigm is particularly suitable for studying Fitts' law in an fMRI setup, as it does not require an actual motor response, ensuring that the observed results cannot be due to motor production confounds or movement-related artifacts.



**Figure 3.1:** Stimuli examples for ID2-W8 combination. Left panel: human movement as depicted by a hand moving between two identical targets. Right panel: object movement depicted by a pen moving between two identical targets.

Each trial began with a blank screen (500 ms) followed by a fixation cross (1000 ms), after which the stimulus pair was presented (Figure 3.2). Each still frame remained on the screen for 500 ms, producing three different sequence durations, 2000, 3000, or 4000 ms for the 2-, 3-, or 4-cycle sequences respectively. Pilot data showed that 4 cycles were sufficient to induce an apparent motion. The length of the trials varied to facilitate the estimation of the HRF response per trial and also to ensure that events did not alternate at a fixed frequency, as the latter are usually associated with noise. The participants' task was to estimate the relative speed of the movement: (1) very slow, (2) slow, (3) fast, and (4) very fast. To prevent stimulation of the motor regions by response requirements, the participants did not respond in 80% of the trials. In the remaining 20% of trials, a question appeared on the screen following the stimuli pair, asking the participants to rate the speed of the observed motion by using the button box placed inside the scanner. The participants could not tell while watching the movement whether the prompt question would follow. The participants had a maximum of 4000 ms to respond to the question, and as soon as a response was collected, the next trial commenced. These randomly presented "catch" trials were included to ascertain participants' attention and were modeled separately in the data analysis.



**Figure 3.2:** An example catch trial of the task presented in the scanner. Response collection is included only in catch trials.

The experiment consisted of 450 trials ( $= 3 \text{ ID} \times 3 \text{ W} \times 2 \text{ movement type, left-hand/right-hand OR object, repeated 25 times}$ ), presented in random order. To provide opportunities for pauses, the experiment was run in six blocks with 75 trials. Each block lasted for approximately 6 min. In order to increase efficiency, no null events were included in this experiment, as our main interest was to identify neural modulations in response to changes in ID (i.e., differences between conditions, rather than differences between a condition and a baseline). To present the stimuli and register event times, we used E-Prime (Psychology Software Tools, Pittsburgh, PA, USA).

*fMRI data acquisition.* We used a Philips 3T Achieva system (Philips Medical Systems, Best, The Netherlands) to acquire blood-oxygen-level-dependent (BOLD) contrast-weighted echo-planar (EPI) for the functional scans. We acquired 38 slices, 2-mm-thick, with a 1.25-mm gap, resulting in an in-plane resolution of  $2 \times 2$  mm, with an  $80^\circ$  flip angle, 35-ms echo time, and 2110-ms slice repetition time (TR). Images were acquired with an eight-channel phased array coil with a sense factor of 2. To minimize susceptibility artifacts, shimming was performed for each acquisition run, and the slices were tilted along the frontal-temporal cortex (Deichmann, Gottfried, Hutton, & Turner, 2003). The slices covered the entire brain, including the parietal cortex and the cerebellum.

*fMRI data analysis.* Whole-brain, voxel-based analysis was done with SPM5 (Wellcome Department of Imaging Neuroscience, London, UK, [www.fil.ion.ucl.ac.uk/spm](http://www.fil.ion.ucl.ac.uk/spm)). In preprocessing, the EPI volumes were first spatially realigned to correct for movement artifacts (Ashburner & Friston, 2003a) and motion by distortion interactions (Andersson, Hutton, Ashburner, Turner, & Friston, 2001). The volumes were then transformed to the Montreal Neurological Institute (MNI) standard space (Ashburner & Friston, 2003b) and smoothed with a 9-mm Gaussian kernel to account for residual intersubject differences and to accommodate assumptions of random field theory used for family-wise error corrections (Worsley & Friston, 1995).

*Linear effects of ID change.* First-level analysis consisted of modeling single-subject BOLD responses in a design matrix that included the onset and duration of stimulus pairs for 18 conditions ( $3 \text{ IDs} \times 3 \text{ Ws} \times 2 \text{ movement conditions}$ ). Note that the A values (the distance between two targets) are determined by W and ID. Therefore, these were not modeled directly. In order to ensure that motor output could not affect differences in brain activation across conditions, catch trials were modeled separately and not included in further analyses.

The regressors in both models were convolved with two basis functions: the canonical hemodynamic response function (Friston, Harrison, & Penny, 2003) and

its derivative that captures fluctuations in response onset (Friston, Fletcher, Josephs, Holmes & Rugg et al., 1998). To correct for signal changes due to residual head movement artifacts, the six realignment parameters were included in the design matrix. Low temporal fluctuation in the data was modeled with a set of harmonic vectors (high-pass filtering 1/128 Hz) likely to be associated with scanner and physiological noise (Josephs & Henson, 1999).

Linear contrasts pertaining to the effects of ID, W, A, and motion type were computed. For an effect of increasing ID, we computed the following two contrasts per each subject: ID2 < ID3, ID3 < ID4. We also used the same technique for effects of increasing width—W2 < W4, W4 < W8—and for amplitude—A4 < A8 < A16 < A32 < A64 (the linear effect size of the covariates) (Table 3.1). The effect of movement type was computed by comparing responses during human movement to those during object movement.

To allow for inferences at population level, secondlevel analyses (separate for ID, W, A, and movement type) were computed with the contrast images created at the first level. A neural effect of increasing ID was tested by the conjunction (with global null: Friston, Penny & Glaser, 2005) of ID2 < ID3 and ID3 < ID4. Note that the conjunction analyses used two orthogonal contrasts and ensured that we report only regions that showed an increased activation for ID at both levels (from ID2 to ID3 and ID3 to ID4). A similar conjunction analysis was performed for W (target width). It should be noted that these analyses did not assume any linear change. We also looked at the linear effect size for A (distance between targets). We report clusters, at  $p < .001$  uncorrected, that were larger than 30 mm<sup>3</sup>, unless otherwise specified (see supplementary materials). The entries represent the estimated response extracted from the first eigenvariate of a 6-mm<sup>3</sup> sphere centered on the maxima group response.

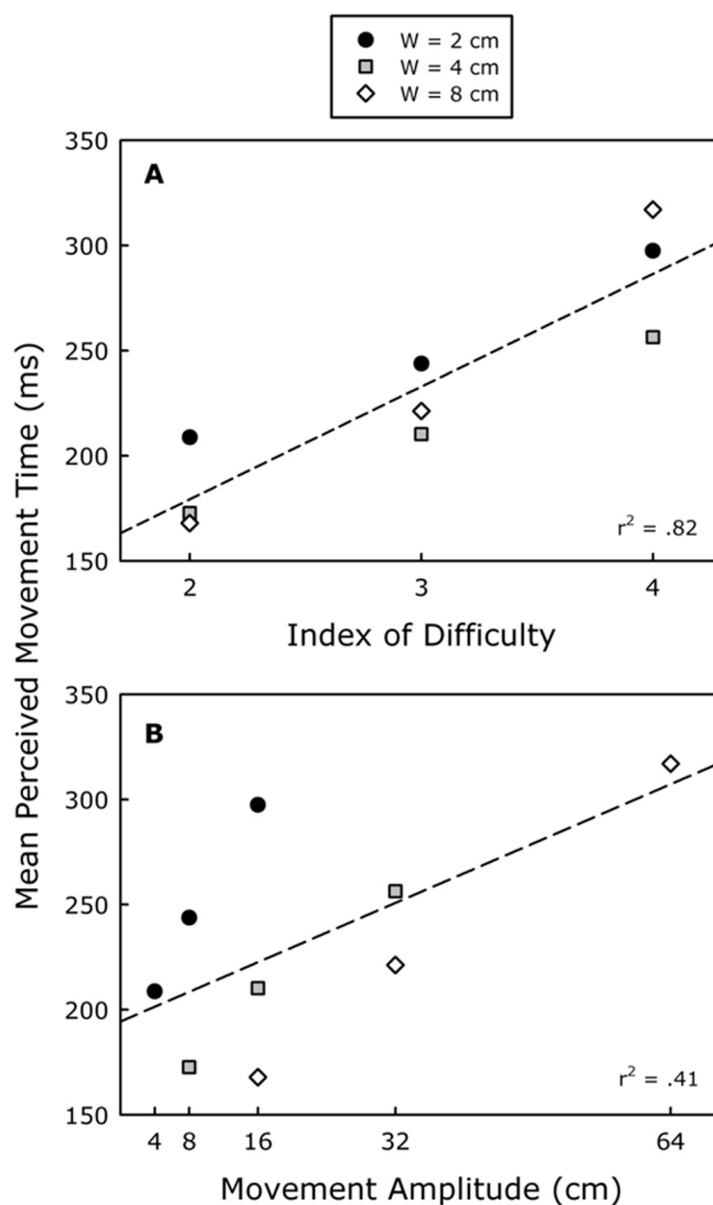
## Results

### Behavioural data

Figure 3.3 (panel A) depicts mean perceived movement time (MT) as a function of ID and W. As expected, ID was a significant predictor of perceived MT:  $r^2 = .82$ , perceived MT =  $72.1 + 53.6 \times \text{ID}$ ,  $F(1, 7) = 32.00$ ,  $p < .001$ . That is, mean perceived MT increased linearly with the ID of the observed movement. Top panel of Figure 3.3 presents the same data plotted as a function of A instead of ID. As can be seen, A alone was not a good predictor of perceptual performance:  $r^2 = .41$ , perceived MT =  $194.4 + 1.8 \times A$ ,  $F(1, 7) = 4.93$ ,  $p = .062$ . These results replicate the findings of Grosjean et al. (2007) and are consistent with Fitts' law.

### fMRI data

There were no above-threshold differential brain responses to left and right-hand movements. Therefore, these two conditions were collapsed. Our main aim was to identify the neural structures that show a change in activity in response to an increase in ID, the main parameter of Fitts' law. We hypothesized that this information would be processed in structures known to be related to motor control. We predicted that these structures would show increased activation in response to an increase in ID of observed human movement, but not in response to an increase in W or A changes. To ensure that our results reflected a gradual increase of ID rather than being driven by the two extremes (i.e., ID2 vs. ID4), we used a conjunction analysis that tested for increases from ID2 to ID3 and ID3 to ID4. Results are reported with a mixed threshold approach with a peak height of  $z > 3$  and a cluster size ( $p < .001$ ) of 30 mm<sup>3</sup> (Poline, Worsley, Evans, & Friston, 1997).



**Figure 3.3:** Mean perceived movement times as a function of target width (W) and (A) index of difficulty (upper panel) and (B) movement amplitude (lower panel). The corresponding linear regression lines and coefficients of determination are also provided.

The results yielded increased activity in regions associated with motor execution and motor preparation, as ID of the perceived movement increased (Table 3.2 and Figure 3.4): central sulcus, SMA, precentral sulcus, and basal ganglia/globus pallidus (GP). In all these regions, the correlation of BOLD responses to changing ID occurred only in the human movement condition, and not in the object-movement condition. We note that at a cluster level, the effects for a change between ID2 < ID3 in the bilateral basal ganglia, left central sulcus, SMA, precentral sulcus, and GP survived family-wise error correction ( $p < .05$ ; with voxel peak  $p < .01$  and clusters extent > 500 voxels). Unfortunately, cluster-level corrections cannot be reliably applied to conjunction analysis (Friston, Holmes, Price, Buechel, & Worsley, 1999).

No effect of ID was observed in these regions for the object-movement condition ( $p > .05$ ). This was tested by exclusive masking with the ID change for object-movement contrast. Furthermore, the activation in the CS, SMA, left precentral sulcus, and GP overlapped with regions that responded more strongly to human movement than to object movement, (tested by inclusive masking,  $p < .05$ ). This provided further evidence that the neural structures involved in computing ID were also more likely to respond to human movements than object movements (Figure 3.5, also see supplementary materials). Importantly, activity in motor regions was observed despite the fact that participants were not executing any motor responses in these trials. There were no above-threshold activations that varied with ID in object-movement trials.

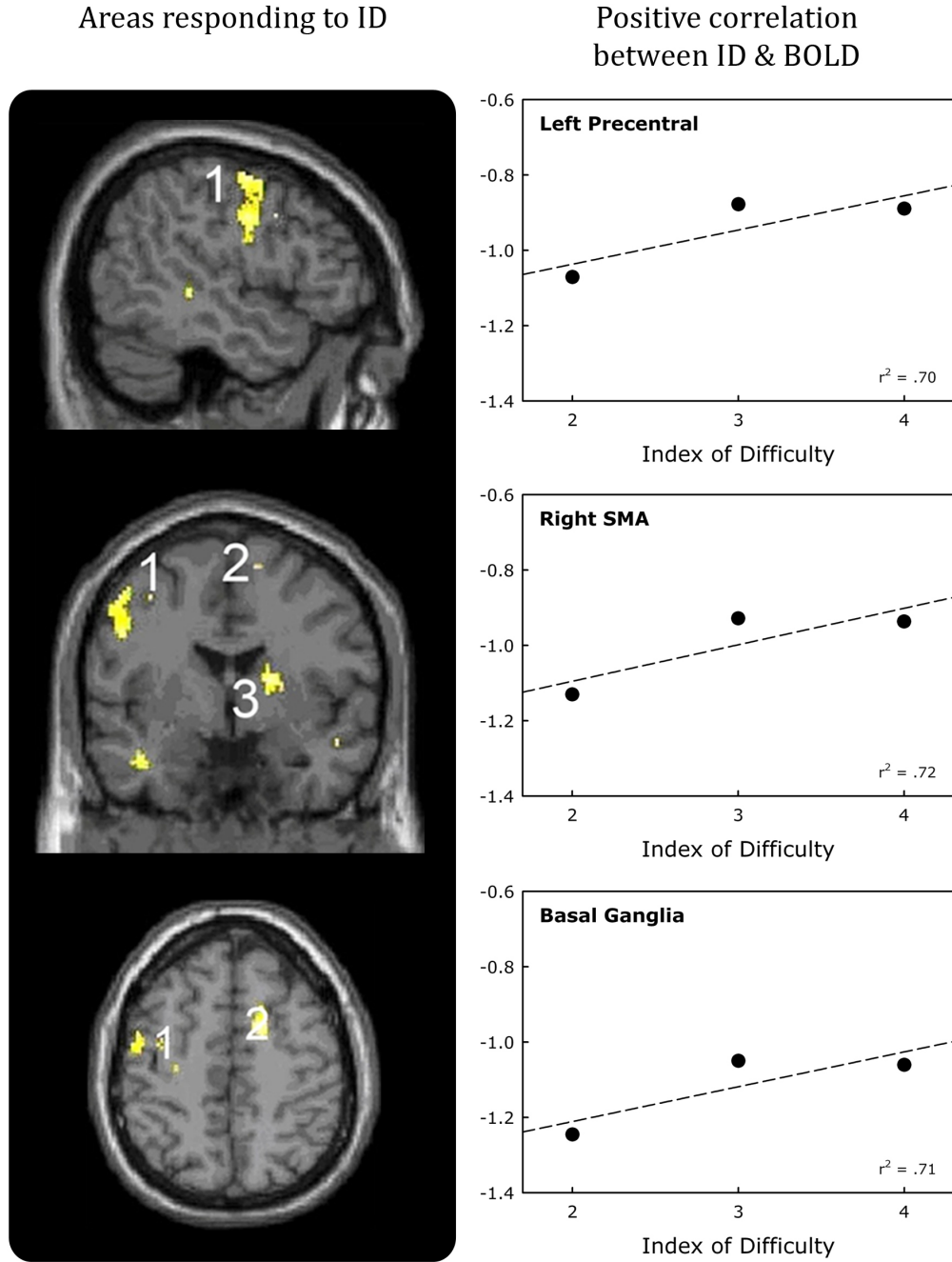
Further analyses showed that brain activation did not significantly increase in response to different amplitudes (A,  $p > .01$ , uncorrected) and different target size (W,  $p > .01$ , uncorrected). We also looked at the possible effects of decreasing ID (Winstein, Grafton, & Pohl, 1997). A similar conjunction analysis to that above was performed. However, this time, the contrast images were set up in the opposite direction (i.e., ID4 < ID3, ID3 < ID2). This analysis did not reveal any significant clusters at a threshold of  $p > .01$ , uncorrected. A weak effect of decreasing amplitude was observed, suggesting an increase in responses as the two targets were located



closer to each other. This was observed in the left extrastriate cortex (BA 18, MNI: -18, -72, -2,  $z = 3.43$ ,  $p < .001$ , cluster = 30 mm<sup>3</sup>), the left lateral orbitofrontal cortex (BA 47, MNI: -40, 50, -8,  $Z = 3.77$ ,  $p < .001$ , cluster = 76 mm<sup>3</sup>), and the medulla (MNI: -4, -18, -32,  $z = 3.89$ ,  $p < .001$ , cluster = 98 mm<sup>3</sup>). This effect may potentially relate to visual crowding. Finally, there was no above-threshold response for decrease in target width ( $W$ ,  $p > .01$ ).

## Discussion

This study aimed to identify the neural structures sensitive to increasing difficulty (ID) of an observed action, as expressed by Fitts' law. The main finding was that activity in motor areas varied in response to increasing ID. These areas included the primary motor cortex, the right supplementary motor area, and the GP. This finding is further supported by a repetition-suppression analysis: Activation in these areas was suppressed as the same ID was repeated in the subsequent trial. As predicted, this pattern of activity in the motor system was observed only in the human-hand condition and not in a moving-object condition (Figure 3.5), showing that it was essentially biological action that engaged the motor system (Urgesi, Moro, Candidi, & Aglioti, 2006; but cf. Grosjean et al., 2007). We also found that neurons in the SMA, M1, and GP were sensitive to the repeated levels of ID, showing a diminished response when ID level was repeated compared to when it changed. Again, this effect was specific to the human-movement condition. Finally, the  $W$  (target width) or the  $A$  (movement amplitude) variables did not reveal any differential activations. It should be stressed that the task used here manipulates ID orthogonally to the perceptual differences across conditions. In other words, the same ID level could be achieved through different  $W$  and  $A$  combinations.

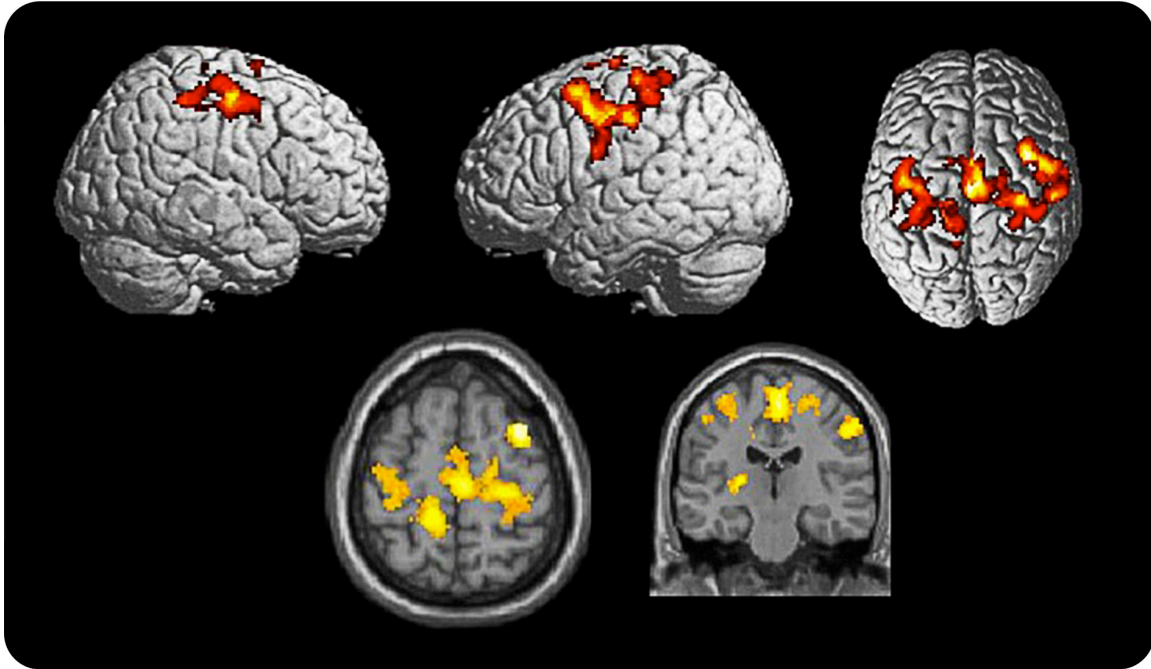


**Figure 3.4:** Display of the conjunction SPM maps on a single-subject template T1: for human movement conditions, ID2 < ID3 and ID3 < ID4, at a combined threshold of maxima ( $z > 3$ ) and cluster ( $p < .001$ ) larger than 30 mm<sup>3</sup>. Areas that are sensitive to increasing ID are 1. left central sulcus (-48, -8, 54), 2. Right SMA (18, 4, 50), and 3. right basal ganglia (globus pallidus; 20, -2, 12). The scatter plots on the y-axis the relative effect size for that region per each condition (arbitrary units) and on the x-axis the index of difficulty (ID).

**Table 3.2:** Conjunction analysis, human movement ID2<ID3 and ID3<ID4.

Min-t(8) is size of the smallest of the effects from the two comparisons. We report clusters at  $p < .001$ , uncorrected, that were larger than 30 mm<sup>3</sup>. Index: SMA, supplementary motor area; pCS, precentral sulcus; CS: central sulcus; aCG: anterior cingulate gyrus, globus pallidus; SN: substantia nigra; MTC: middle temporal cortex; aTP: anterior temporal pole; L: left hemisphere; R: right hemisphere.

Anatomical region		MNI coordinates			Cluster size	Min-t(8)	Z
		x	y	z			
<i>[ID2&lt;ID3] &amp; [ID3&lt;ID4]</i>							
<i>Frontal</i>							
SMA	R	18	4	50	421	2.73	4.11
pCS	L	-40	8	42	2076	2.64	4.01
CS	L	-48	-8	54	2076	2.56	3.91
aCG	L	-10	44	10	86	2.19	3.45
Superior orbital gyrus	L	-16	20	-8	339	2.49	3.82
<i>Sub-Cortical</i>							
Globus pallidus	R	20	-2	12	184	2.62	3.98
Pons	L	-6	-42	-28	147	2.35	3.65
SN	R	10	-18	-24	223	2.33	3.62
Amygdala	R	24	8	-22	366	2.6	3.96
Hippocampus	L	-24	-14	-16	473	2.4	3.71
<i>Occipital and Temporal</i>							
4th occipital	L	-12	-82	-8	165	2.49	3.82
Calcarine	R	10	-88	12	807	2.38	3.69
	L	-18	-96	12	196	2.34	3.64
MTC	R	50	-24	-14	81	2.26	3.54
aTP	L	-40	-2	-26	473	2.4	3.71
	R	50	0	-18	366	2.31	3.6



**Figure 3.5:** SPM maps for (human movement condition > object movement condition) displayed on a rendered brain and on a single subject template T1, at a combined threshold of maxima ( $z > 2.5$ ) and cluster ( $p < 0.05$ ) larger than  $200\text{mm}^3$ .

The brain areas that showed differential activation as a function of ID have also been shown to be involved in different types of action simulation, including motor imagery. Chiefly, the M1 is well known for its contribution to observation of actions (Grèzes & Decety, 2001; Munzert, Zentgraf, Stark, & Vaitl, 2008; Porro, Francescato, Cetollo, Diamond & Baraldi et al., 1996; Roth, Decety, Rayboudi, Massarelli & Delon-Martin et al., 1996). The SMA, an area involved in simulation of motor sequences (Grafton, Arbib, Fadiga, & Rizzolatti, 1996), is a part of an overlapping network between motor imagery and action observation (Lotze, Laubis-Herrmann, Topka, Erb, & Grodd, 1999; Munzert et al., 2008; Zentgraf, Stark, Riser, Kuenzell & Schienle et al., 2005). The GP, a structure within the basal ganglia, has also been shown to be active during imagination and observation of movements (Gerardin, Sirigu, Lehighy, Poline & Gaimard et al., 2000; Munzert et al., 2008).

Surprisingly, we found no differences in cerebellar activity. The cerebellum has been implicated in internal models, specifically with respect to predictive timing in executed as well as simulated actions (Imamizu, Miauchi, Tamada, Sasaki & Takino et al., 2000; Wolpert et al., 1998). This could perhaps be due to lack of speed differences in the observed movements. In order to avoid the confound of perceived speed, it was kept constant across different levels of IDs. Therefore, speed was always perfectly predictable, and this may explain why there were no differences in activation in the cerebellum. Thus, it is likely that the modulation of basal ganglia activation that was observed as a function of ID was also not due to differences in timing, although it is known that the basal ganglia play an important role in the timing of movements (Ivry & Spencer, 2004; Lewis & Miall, 2003). We have recorded an activation increase in response to increasing levels of difficulty occurring in the right GP, a locus encompassing both internal and external GP (right GPi and GPe). Numerous neuroimaging studies, as well as lesion studies on neuropsychological patients (e.g., Parkinson's, Huntington's, and dystonic patients) show that these two nuclei of basal ganglia are important in regulating force control in produced actions (Aparicio, Diedrichsen, & Ivry, 2005; Prodoehl, Corcos, & Vaillancourt, 2009). More specifically, GPi activity has been found to parametrically scale with the rate of change in force production, and it has been suggested that the basal ganglia have a direct influence on hand representations of M1 (Prodoeh et al., 2009). Accordingly, the present results suggest that the observation of hand movements of varying difficulty scaled activation in a motor area that is specifically involved in hand force production.

It may seem surprising that the ID manipulation did not affect brain areas that have been described as the human mirror system (Rizzolatti & Sinigaglia, 2010). Whereas studies on mirroring in humans have demonstrated overlaps in neural activation between observed actions and corresponding motor representations in the observer, the present study manipulated a specific parameter of this match: the ID of the observed action. Thus, the differences in activity reflect how the motor system is modulated once a perception action match is established. Consistent with this

reasoning, an early PET study that addressed the influence of ID on brain activation during task execution (Winstein et al., 1997) found a similar pattern of neural activity as the present study and no activation in the human mirror system.

The present results support the assumption that motor simulations are sensitive to motor parameters (ID) rather than perceptual parameters. The simulated difficulty of performing the action oneself (ID) rather than the perceptible differences in target size (W) or distance (A) drive motor system activation. Combining these results together with the lack of mirroring activity, one can speculate that human mirror circuitry was active throughout the experiment, thus allowing the motor system to run predictive forward models (Wilson & Knoblich, 2005) to simulate a particular motor parameter. The present findings might indicate that action perception is a complex process going beyond mere recognition of an action. Action perception seems to involve simulation of specific motor aspects of an observed action, and is supported by regions that extend beyond the human mirror circuitry.

In sum, the present study provides a neural basis for explaining previous findings where effort scales the perceived difficulty of observed or imagined actions (Delignières, 1998; Gopher & Braune, 1984) in different environmental conditions (Witt et al., 2005). To conclude, the present study adds to the body of converging evidence supporting tight links between perception and action. It provides clear evidence that the same constraints that govern motor performance during action execution also govern simulations in the motor system during action observation. Thus, when people observe others acting, they simulate the difficulty of the perceived actions by matching them to their own action repertoire. Whether this implies that we become exhausted when we observe others work hard remains to be explored.

## Supplementary Materials

The analysis of the behavioural-task data was identical to that employed by Grosjean et al. (2007). Using maximum-likelihood estimation, a logistic function ( $y = 1/[1 + e^{[a-x]/b}]$ ) was fit the proportion of “possible” judgments as a function of SOA for each  $W \times ID$  combination and participant. The SOA that corresponded to a proportion of 0.5 of “possible” judgments was then defined as the perceived MT for that combination and participant. For two participants, the logistic function could not be fit for some of the  $W \times ID$  combinations ( $M = 2.50$ ) because the movements were almost always judged as “possible”, independent of SOA. These missing values were replaced with the overall mean perceived MT for that participant, which is a conservative replacement method (Grosjean et al., 2007).

For the analysis of the fMRI data, we tested whether observing human movements elicited differential responses than observing an object move. A combination of maxima size ( $z > 2.4$ ) and cluster size (cluster ( $p < 0.05$ )  $> 200 \text{ mm}^3$ ) was taken as threshold. As expected larger responses were observed in bilateral central sulcus, supplementary motor cortex (SMA), right lateral middle frontal cortex and left thalamus and basal ganglia (Supplementary Table 3.1, Figure 3.5). Note that the responses in motor associated regions were observed despite the fact that observer did not execute any overt motor response. There were no above threshold responses for the opposite comparisons. This accords with many previous studies (Buccino, Binkofski, Fink, Fadiga & Fogassi et al. 2001; Ehrsson, Spence & Passingham, 2004) showing an increased response in motor regions when watching human hand movements.

**Supplementary table 3.1.** Human movement > Object movement. Index: MFG, middle frontal gyrus, SMA, supplementary motor area, CS, central sulcus, BG, basal ganglia, R, right, L left.

Anatomical region		MNI coordinates			Cluster size	<i>p</i>	<i>Z</i>
<i>Human Movement &gt; Object Movement</i>							
MFG	R	36	10	60	53	.003	2.8
SMA	R	4	-18	68	78	.003	2.7
CS	R	54	-20	42	5	.006	2.52
	L	-14	-34	50	4	.007	3.14
Thalamus and BG	L	-22	-18	10	9	.005	3.37





## Chapter 4

# You: Does sharing tasks affect memory encoding?

A version of this chapter is published as:

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## **Abstract**

Social influences on action and memory are well established. However, it is unknown how acting together affects the incidental encoding of information. The present study asked whether co-actors encode information that is relevant to a partner's task, but irrelevant to their own task. In Experiment 1, participants performed a categorization task alone and together, followed by a surprise free recall test where they were asked to recall items from the categorization task. Recall was not only better for items participants had responded to themselves, but also for items their co-actor had responded to, compared to items that had not required a response. The same results were found in Experiment 2, even though financial incentives motivated participants to only encode words they had responded to themselves. Together, the findings suggest that performing tasks together can modulate how information relevant to co-actors is processed. Shared task representations may act as a vehicle for establishing shared memories.

## Introduction

Studies on action and studies on memory suggest that the human mind is attuned to others. Previous research on action has shown that individuals take into account each other's tasks even when they perform independent reaction time tasks alongside each other (e.g., Atmaca, Sebanz, & Knoblich, 2011; Milanese, Iani, & Rubichi, 2010; Sebanz, Knoblich & Prinz, 2003; 2005; Welsh, Elliott, Anson, Dhillon & Weeks et al., 2005). For instance, a response selection conflict between a left and a right response was observed in participants who only controlled a right response option when they were sitting next to a person taking care of the left response (Sebanz et al., 2003). Such effects of 'task sharing' have been found regardless of whether or not the other's actions can be observed. The mere belief to be acting together with an intentional agent can be sufficient (Atmaca, et al., 2011; Ruys & Aarts, 2010; Stenzel, Chinellato, Tirado, Bou & del Pobil et al., 2012; Tsai, Kuo, Hung & Tzeng, 2008).

It has been suggested that people form a representation of their co-actor's task that specifies which events require the other to act (Wenke, Atmaca, Hollaender, Liepelt & Baess et al., 2011; so that seeing stimuli that are potentially task-relevant for the other activates a representation of the other's task and thereby induces a response selection conflict (Kiernan, Ray & Welsh, 2012; Milanese et al., 2010; Welsh, 2009; but see Guagnano, Rusconi & Umiltà, 2010 for an alternative spatial coding account, and Liepelt, Wenke & Fischer, 2012; Liepelt, Wenke, Fischer & Prinz, 2011 for a feature binding account). Recent findings show that a co-actor's task can also change stimulus processing even when there is no response conflict (Boeckler, Knoblich, & Sebanz, 2012).

Studies on social influences on memory suggest that people cannot help taking into account others' memories when recalling information together. For example, when collectively retrieving material that had been learned individually, people tend to

forget information that their partner has omitted (Cuc, Koppel & Hirst, 2007; Coman, Manier & Hirst, 2009). By the same token, people report information that their retrieval partners produced, as if it were part of what they had learned alone (for a review, see Loftus, 2005). For instance, when participants were asked to watch different versions of a story, and then tested individually following a collective recall protocol, they remembered items from both versions (Gabbert, Memon & Allan, 2003). This effect of sharing of memory persists even when people are warned against it (*ibid.*). The effect is more pronounced when the novel information is injected by another person, compared to when it is presented as written text (Meade & Roediger, 2002), together suggesting that there are mechanisms of social interaction that foster the involuntary sharing of memories.

The above studies demonstrate social effects on retrieval by showing that collective retrieval affects subsequent recall of information that has previously been encoded individually (Roediger, Meade & Bergman, 2001). Studies on transactive memory have investigated how pairs of people memorize information when asked to later recall it together (Wegner, 1986; Wegner, Erber & Raymond, 1991). However it is largely unknown how acting together affects the way information is incidentally encoded when there is no intention to perform a joint memory task. When performing a task together with another, does representing the co-actor's task affect the way information relevant to the co-actor is processed and consequently how it is later recalled? Do people encode information that requires their partner to act, but not themselves? If co-actors take each other's tasks into account, representing which stimuli call for an action by the other (*cf.* Knoblich, Butterfill, & Sebanz, 2011 for a review of the evidence), then memory should not only be improved for items that require oneself to act (Nilsson, 2000; Noice & Noice, 2001), but also for items that require the other to act. Accordingly, information that is task-relevant for one's partner should be better recalled than information irrelevant to one's own or the other's task.

The present study examined how well individuals are able to recall information that required their own action, a co-actor's action, or no action during an earlier performed categorization task. In Experiment 1, participants performed the categorization task alone and together without knowing that their memory would later be tested. In Experiment 2, participants believed that they would be rewarded for recalling items they had responded to themselves, thus creating a strong incentive to focus on their own items and to ignore the other's items.

### **Experiment 1**

This experiment tested whether people performing independent categorization tasks show improved memory performance for items that require their co-actor's response. Participants first performed a categorization task alone and together. In the joint condition, each participant in a pair responded to words of one category (e.g., one person responding to animals, the other to household items). Words of a third category (e.g., fruit and vegetables) did not require a response and served as a control. In the individual condition, participants responded to words from their own category and not to words from the other two categories (e.g., responding to animals, but neither to household items nor to fruit/vegetables). Following the individual and joint categorization tasks, participants were asked in a subsequent individual surprise test to recall as many items as possible, regardless of whether they had encountered them alone or together, and regardless of whether they, their co-actor, or nobody had responded to them.

In line with previous findings, we expected recall to be best for those items that required the participants to act themselves (Nilsson, 2000; Noice & Noice, 2001). The main question, however, was whether acting together would improve recall for items that did not require participants' own action, but required their partner's action. This can be tested in two ways. Firstly, words that required the partner to act (joint condition, 'other') should be better recalled than words of the same category that were encountered alone (individual condition, 'other'). Secondly, words that required the partner to act (joint condition, 'other') should also be remembered

better than words from a different category that did not require anyone to act (joint condition, ‘no one’). If participants generally recalled more (or less) items from the joint task than from the individual task, regardless of whether an item required their own response, the co-actor’s response, or no response, this would suggest a more general effect of acting together, known as social facilitation (Aiello & Douthitt, 2001).

## Method

*Participants.* 48 participants from Rutgers University, USA, took part in this experiment in exchange for course credit or monetary compensation.

*Materials and Procedure.* Participants were recruited as pairs, and received instructions together. In the first part, participants performed a categorization task alone (individual condition) and together in a pair (joint condition). Each participant was assigned one of three word categories (animals, fruit/vegetables, household items), and was instructed to respond only to items belonging to their assigned category by pressing the indicated key (e.g., participant A responded to animals, participant B to household items). The order of conditions was counterbalanced, so that half of the participants performed the individual condition first, and half performed the joint condition first. Participants were told to do nothing in response to items of the other, unassigned categories. All categories were mentioned equally often in the individual and in the joint condition.

The stimulus materials comprised a total of 192 word items that were divided into two sets. Half of the experimental sessions used one set, the other half used the second set. In each experimental session 96 stimuli were shown. The stimuli for each of the three word categories consisted of 32 items that were matched for frequency (Kucera & Francis, 1967). Half of the items of each category were presented in the individual condition and half were presented in the joint condition. Throughout the experiment, the item category and the response key assigned to each participant remained the same (e.g., participant A responded to animals with

key 'z' in both conditions). An equal number of participants was assigned to each of the three categories, and all combinations of categories across participant pairs (e.g., Participant A responding to Animals, Participant B responding to household items) occurred equally often. For instance, for Pair 1, participant A and participant B were assigned to animal and fruit/vegetable items, respectively, and household items were not assigned, whereas for Pair 2, participant A and participant B were assigned to fruit/vegetable and household items, and animal items were not assigned. Two keys on the computer keyboard were assigned for making the responses, one for each participant. The response key-category pairings were counterbalanced across participant pairs so that for instance half of the participants responding to animals used the key 'z', and half used the key 'm'. The experiment was run on an Apple Power PC using PsyScope (Cohen, MacWhinney, Flatt & Provost, 1993).

Participants in the joint condition sat next to each other on chairs that were at fixed positions to the left and right of the computer screen and used the same keyboard to respond. In the individual condition one of the chairs remained empty. Each trial commenced with a 500 ms fixation cross, followed by the stimulus presented for 1500 ms. Participants pressed a key as quickly as possible if an item of their assigned category was displayed and did not press a key for any other items (performing a go/no-go task). From the perspective of each participant one third of the trials required a response ('self'), one third of the trials never required a response ('no one'), and one third required a response from the other in the joint condition and no response in the individual condition ('other'). In the second part of the experiment, participants performed a surprise free recall test. They were tested alone and were asked to write down as many of the previously encountered items as possible (regardless of category) within 2 minutes. A pilot study had shown that this provided ample time.

## Results and Discussion

We analyzed the number of items that were recalled (see Figure 4.1, Table 4.1). Firstly, to analyze recall for items that had required the participant to respond, a 2 x

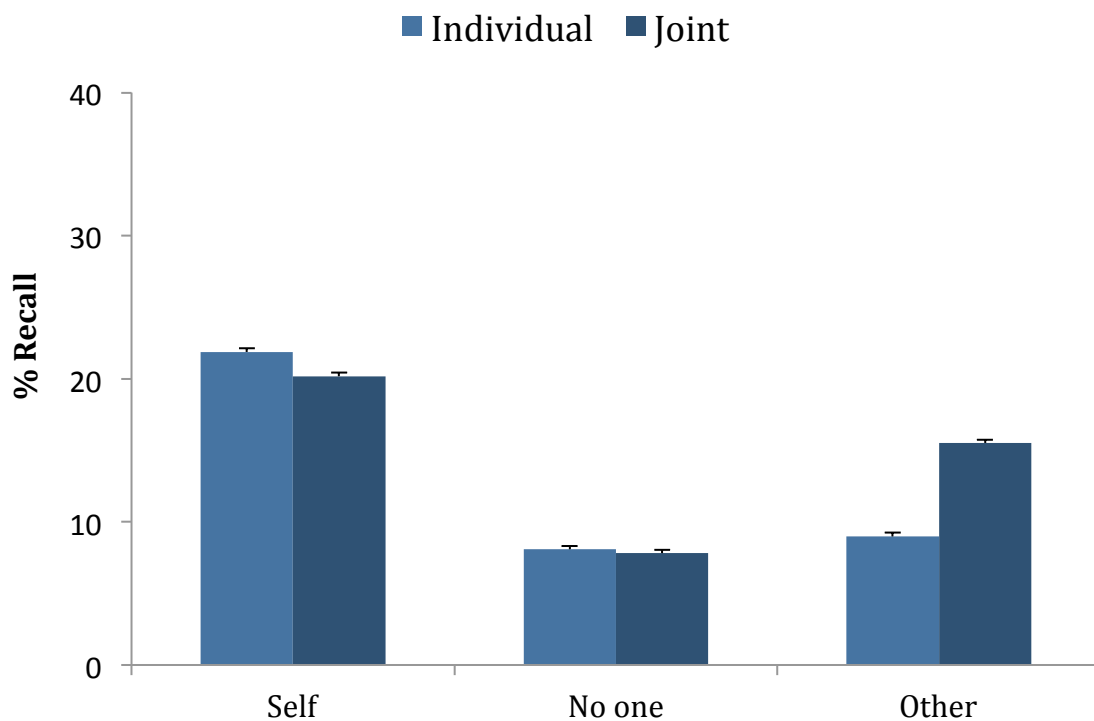


2 ANOVA with the within-subjects factors Condition (individual vs. joint) and Category ('self' vs. 'no one') was conducted. There was no main effect of Condition, but the main effect of Category was significant ( $F(1, 47) = 88.0, p < .001, \eta_p^2 = .65$ ). The interaction was not significant ( $F(1, 47) = .24, p = .63, \eta_p^2 = .005$ ). Participants recalled more of the items they had responded to, compared to items no one had responded to, regardless of whether these items had been encountered individually or jointly.

Our main prediction was that words that required a co-actor to respond (joint, 'other') should be recalled better than the words that required no one to respond (individual, 'other'; individual, 'no one'; joint, 'no one'). To test this a 2 x 2 ANOVA with the within-subjects factors Condition (individual vs. joint) and Category ('other' vs. 'no one') was performed. Both main effects and the interaction were significant (Condition:  $F(1, 47) = 4.1, p < .05, \eta_p^2 = .8$ ); Category:  $F(1, 47) = 16.6, p < .001, \eta_p^2 = .26$ ; interaction:  $F(1, 47) = 11.2, p < .01, \eta_p^2 = .19$ ). Two-sided t-tests confirmed that participants recalled significantly more items from the category assigned to the co-actor when the co-actor had responded to these items (joint condition, 'other') than when the co-actor was absent and had not responded to them (individual condition, 'other',  $t(47) = 3.07, p < .01$ ). Recall for items the other had responded to (joint condition, 'other') was also significantly better than recall for 'no one' items in the joint condition, ( $t(47) = 4.58, p < .001$ ), and in the individual condition ( $t(47) = 3.59, p < .001$ ). The order in which the individual and the joint condition had been performed did not affect the results (no significant main effect of order and no significant interactions involving order). Taken together, the results of Experiment 1 show that surprise free recall of a co-actor's items was improved.

**Table 4.1:** Mean percentages for recalled items for Experiments 1&2.

Items	Experiment 1		Experiment 2	
	Individual (%)	Joint (%)	Individual (%)	Joint (%)
Self	21.8	20.2	37.5	37.8
No one	8.0	7.8	7.0	8.9
Other	8.9	15.5	7.6	16.4



**Figure 4.1:** Mean percentage of words recalled in Experiment 1. Words belonging to a coactor's category were recalled more frequently when participants had performed a joint task rather than an individual task. Error bars reflect within-subject confidence intervals (G. R. Loftus & Masson, 1994).

## Experiment 2

Experiment 2 tested whether better recall for items requiring a co-actor's response would still occur when it pays off to focus on one's own task. To create a strong motivation for participants to encode only items of their own category, they were led to believe that they would be paid for each word recalled from their own category. However, after the categorization part of the experiment they were asked to recall any item previously encountered, just like in Experiment 1.

### Method

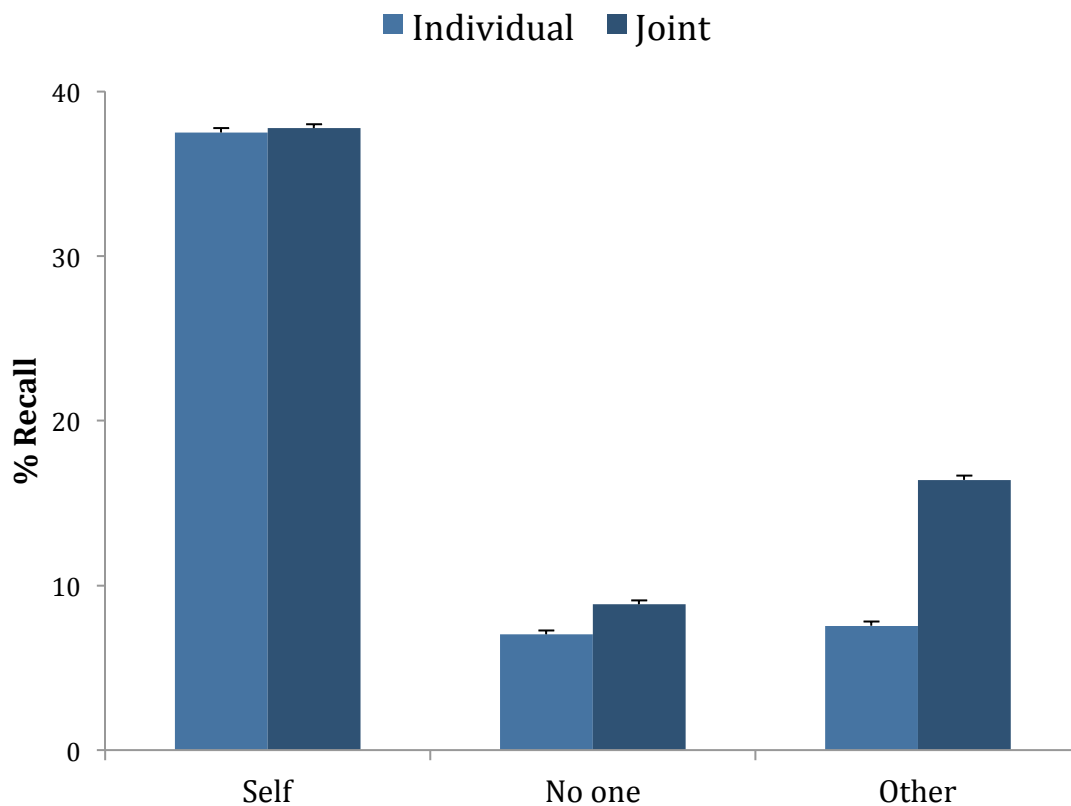
*Participants.* 24 participants were recruited from the University of Birmingham in exchange for course credit or monetary compensation.

*Materials and Procedure.* This experiment differed from Experiment 1 only in terms of instructions. Participants were told at the beginning of the experiment that there would be a free recall test after the categorization tasks and that they would be tested only on the items they had responded to, i.e., items from their own category. They were explicitly instructed to focus on these items and they were told that they would receive 10p for each correctly recalled word. However, after participants had completed the categorization task (individually and jointly), they were asked to recall as many items as possible from any of the three categories. They were paid 10p for each word they could recall from any category, in addition to the fixed compensation rate. Finally, participants were debriefed. All participants reported that they had initially believed that they would only be paid for recalling items from their own category.

### Results and Discussion

The analyses were the same as in Experiment 1. To analyze recall for items that had required participants' own response, a 2 x 2 ANOVA with the within-subjects factors Condition (individual vs. joint) and Category ('self' vs. 'no one') was performed (see Figure 4.2, Table 4.1). It showed a significant main effect of category ( $F(1, 23) =$

126.4,  $p < .001$ ,  $\eta_p^2 = .85$ ). As in Experiment 1, participants recalled more of the items they had responded to, compared to words no one had responded to. The interaction was not significant ( $F(1, 23) = .06$ ,  $p = .81$ ,  $\eta_p^2 = .002$ ).



**Figure 4.2:** Mean percentage of words recalled in Experiment 2. Words belonging to a coactor's category were recalled more frequently when participants had performed a joint task rather than an individual task, despite the monetary incentive to focus on one's own category and ignore the coactor's category. Error bars reflect within-subject confidence intervals (G. R. Loftus & Masson, 1994).

To analyze recall for items the co-actor had responded to a further 2 x 2 within-subjects ANOVA with the factors Condition (individual vs. joint), and Category ('other' vs. 'no one') was conducted. It revealed a significant main effect of Condition ( $F(1, 23) = 10.5, p < .005, \eta_p^2 = .31$ ), and Category ( $F(1, 23) = 6.3, p < .05, \eta_p^2 = .21$ ), as well as a significant interaction ( $F(1, 23) = 4.8, p < .05, \eta_p^2 = .17$ ). Replicating the results of Experiment 1, participants recalled more items when the other had responded to these items compared to items no one had responded to. Two-sided *t*-tests confirmed that participants recalled more items of the other's category when they had appeared in the joint condition than when they had appeared in the individual condition ( $t(23) = 3.77, p < .001$ ). Recall for items the other had responded to was also significantly better than recall for 'no one' items in the individual condition ( $t(23) = 3.65, p < .001$ ) as well as in the joint condition ( $t(23) = 2.9, p < .01$ ). There was no significant main effect of order and none of the interactions involving order reached significance.

## General Discussion

Two experiments confirmed the prediction that joint task performance modulates the encoding of information that is task relevant to a co-actor. Participants were better at recalling items that their partner had responded to, compared to information their partner had not responded to. Recall of the partner's items was improved even though participants were unaware that their memory of the other's items would be tested. Improved recall for the co-actor's items was not only observed when participants did not expect a memory test at all (Experiment 1) but also when they expected to be tested on and rewarded for recalling their own items (Experiment 2). Interestingly, in both experiments, improved recall for the co-actor's items did not seem to come at the cost of reduced recall for items relevant to oneself. Although the joint categorization task resulted in improved recall of the co-actor's items, participants recalled an equal number of their own items regardless of whether they had responded to these items alone or in the co-actor's presence.

The finding of improved recall for items participants had responded to themselves generalizes previous findings on the role of enactment, suggesting that performing a task involving particular items enhances recall of these items even when the link between items and actions is arbitrary (Noice & Noice, 2001; Noice, Noice & Kennedy, 2000). Generating an action plan in relation to a particular item, and monitoring whether the planned action has been correctly executed, may serve to process task-relevant information more deeply and to contribute to episodic memories that later facilitate free recall.

We think it is likely that improved recall for items that were relevant to the co-actor is due to similar mechanisms. Previous research on task co-representation suggests that people form representations of their co-actor's task that specify which items require the other's response (Knoblich et al., 2011; Wenke et al., 2011). When participants perceive a stimulus that requires the co-actor's response (Sebanz et al., 2006a; Tsai et al., 2008) or a stimulus that shares features with the stimuli requiring the co-actor's response (Atmaca et al., 2011; Sebanz et al., 2003, 2005; Vlainic, Liepelt, Colzato, Prinz & Hommel, 2010), an action plan relating to the other's task is activated. Accordingly, when participants saw stimuli requiring the co-actor to respond in the joint categorization task, this likely triggered the activation of an action plan and possibly ensuing monitoring processes (de Bruijn, Schubotz & Ullsperger, 2007).

An open question is whether participants actually engaged in a motor simulation of the actions to be performed by the co-actor. It has recently been shown that seeing someone performing an action can lead to false memories of having performed this action, both in children (Sommerville & Hammond, 2007) and in adults (Lindner, Echterhoff, Davidson, & Brand, 2010). This phenomenon, known as 'observation inflation' is thought to be due to motor simulation, where seeing someone else performing an action activates corresponding motor programs in the observer (Grezes & Decety, 2001; Jeannerod, 2001). If participants in our study simulated performing the co-actor's actions this may have increased the accessibility of items

for recall in a similar way as items they responded to themselves. Given that task co-representation effects tend to occur even when the co-actor cannot be seen (Atmaca et al., 2011; Tsai et al., 2008; Ruys & Aarts, 2010; Vlainic et al., 2010), it will be interesting to explore in future studies whether the present effect depends on the observation of the partner's actions or occurs even when people merely believe that they are performing the categorization task together (Shteynberg, 2010). In the latter case, imagining the other's actions might lead to similar effects as observing them.

We cannot fully rule out the possibility that the co-actor's response provided additional retrieval cues that enhanced recall for the co-actor's items ( Craik & Tulving, 1975). Although, to eliminate response feedback all stimuli remained on screen even after a response by either actor was recorded, key presses could still be seen and heard. These perceptual effects could have potentially increased saliency and/or modulated participants' attention, thus enhancing encoding for a co-actor's items. However, previous studies found preserved task co-representation effects in conditions where participants did not see or hear their co-actor's response (Sebanz et al., 2005; Vlainic, et al., 2010) and even when participants just believed that there was a co-actor (Atmaca, et al., 2011; Ruys & Aarts, 2010; Tsai et al., 2008). Findings from other studies have also demonstrated that neither the mere presence of a co-actor (Sebanz et al., 2003; Tsai et al., 2008) nor receiving the instructions for a potential co-actor's task (Boeckler, Knoblich & Sebanz, 2012) is sufficient for inducing effects of task co-representation. Future studies will be needed to determine the role of online feedback about the other's actions in the present paradigm.

It is unlikely that encoding for the co-actor's items was enhanced because participants suspected that they would have to recall these items. The effect occurred when participants were oblivious to the upcoming free recall test (Experiment 1). One could argue that in Experiment 2, paradoxical effects (Wegner, Ansfield & Piloff, 1998) may have occurred, such that participants focused on non-

self words because they were instructed to focus on their own words. However, if that were the case we should also have found improved recall for ‘no one’ items which was not observed.

Our findings contribute to the understanding of social influences on memory, providing a new link between collaborative memory research (e.g., Barnier, Sutton, Harris & Wilson, 2008) and joint action research (Knoblich et al., 2011; Sebanz, Bekkering, & Knoblich, 2006b). Previous studies on collective recall (e.g. Basden, Basden & Henry, 2000) demonstrated how remembering information together with others reshapes memories. The present study, by manipulating the social context during encoding of information, demonstrates that effects of social interaction on memory are not restricted to retrieval, but also affect encoding. The fact that participants’ memory changed as a function of the co-actor’s task in a context that did not involve verbal communication (Shteynberg, 2010) and did not require collaboration indicates that social effects on memory occur even when people do not intend to encode information together (as in transactive memory paradigms, Wegner 1986; Wegner et al., 1991) or retrieve information together (as in collaborative recall; Basden et al., 2000; Rajaram & Pereira-Passarin, 2007; Weldon & Belringer, 1997; or memory conformity studies; Wright & Schwartz, 2010). In line with findings in the domain of retrieval (Cuc et al., 2007; Coman et al., 2009), our results suggest that processes occurring within individuals may also occur across people, whether this be retrieval-induced forgetting as in the studies by Hirst and colleagues, or improved recall following categorization as in the present case. Most importantly we show that even when the participant’s task does not require paying attention to the co-actor, a co-actor’s task can affect memory performance. It has been suggested that information experienced by those who are socially relevant to us earns prominence and is thus better remembered; this in turn may affect the formation of shared knowledge systems (Shteynberg, 2010). The present findings indicate that people’s proneness to represent others’ tasks may constitute a possible mechanism for the formation of such shared knowledge systems.





## Chapter 5

Them: Does ascribed intentional relations modulate neural processing of observed social intentions?

A version of this chapter is currently under revision as:

Eskenazi, T., Rueschemeyer, S-A., de Lange, F., Knoblich, G. & Sebanz, N. Observing shared intentions in joint action: an fMRI study.

## **Abstract**

Studies on the neural basis of action perception have so far investigated the perception of individual actions. It is still largely unknown how we perceive joint actions where two or more individuals coordinate their actions based on a shared intention. In this fMRI study we asked whether observing situations where two individuals act on a shared intention engages different processes than observing situations where individuals act on their independent parallel intentions. To that end we compared the neural response to perceptually identical yet intentionally ambiguous actions observed in varying contexts. A dialogue between two individuals that conveyed either a shared intention or two independent parallel intentions established the contexts. The dialogues were followed by an identical video clip where the two individuals performed certain actions. We found that compared to observing interactions based on parallel intentions, observing joint actions based on shared intentions activated the temporal poles, precuneus, and the ventral striatum. Precuneus and the temporal poles are thought to support mental state reasoning, the latter with a more specific role in retrieving memories associated with social scripts. We speculate that retrieving social scripts is important for processing joint actions. Activation in the ventral striatum, an area involved in reward processing, suggest that observing shared intentional relations might induce a hedonistic response in the observer similarly to that experienced when personally sharing mental states with others.

## Introduction

To navigate the social world we need to make sense of others' individual actions as well as actions performed jointly by others. To date, research has focused on the processes underlying the perception of others' individual actions. However, from a couple taking a simple walk to a chamber orchestra performing a musical piece, social life abounds with examples of joint actions. Yet little is known about the neural processes underlying the perception of actions performed by multiple people based on a shared intention.

Recent evidence suggests that we are attentionally and perceptually tuned into the joint actions we encounter. For example, even in perceptually impoverished contexts we are readily able to distinguish joint actions from situations where multiple people act on their own (Centelles, Assaiante, Nazarian, Anton & Schmitz, 201; Manera, Becchio, Schouten, Bara & Verfaillie, 2011). Observing two interacting people engages our attention more so than when people are not in any apparent interaction (Boeckler, Knoblich & Sebanz, 2011). This enhanced level of attention in turn facilitates learning, for example, of new words (Akhtar, 2005; O'Doherty, Troseth, Shimpi, Goldenberg, & Akhtar et al., 2011) or actions (Herold & Akhtar, 2008; Nielsen, Moore & Mohammedaly, 2012).

It has also been shown that people draw inferences concerning intentional relations between people they observe. Just as acting in synchrony with others elicits feelings of connectedness and rapport between people (for a brief review, Marsh, Richardson & Schmidt, 2009), we attribute more rapport (Miles, Nind, Macrae, 2009) and a sense of unity ('entitativity', Lakens & Stel, 2011) to those who act in synchrony. We also tend to believe that when others act in synchrony they do so intentionally (Ip, Chiu & Wan, 2006; Lakens, 2010). As early as at 14 months, infants seem to be able to recognize when individuals engage in a complex intentional interaction and work together to achieve a shared goal (Henderson & Woodward,

2011). These studies suggest that we are not only perceptually sensitive to social interactions we observe, but we also have a particular way of reasoning about the mental states of those we observe interacting.

What exactly is the difference between keeping track of jointly performed actions and actions performed by multiple agents acting independently? By definition, joint actions are social instances where two or more individuals spatially and temporally coordinate their actions to bring about a change in the environment (Sebanz, Bekkering & Knoblich, 2006b). In most cases of joint action individuals share an intention to pursue a common goal, which organizes and interlocks their individual intentional actions (Bratman, 1992). In fact some philosophers, although disagreeing on the precise nature of shared intentions, believe that shared intentionality is what characterizes joint actions (Bratman, 1992; Searle, 1990).

Accordingly, when individuals act together with a shared intention this constitutes a different instance than when individuals act in parallel with independent individual intentions. To illustrate the distinction Searle offers the following paradigm case (1990). Imagine a scenario where people are scattered across a park sunbathing. Suddenly rain starts pouring down and people run towards the nearest shelter. Here each individual acts on an intention that is independent from the intentions of others. Imagine a second scenario where the same park is used as a film set and the same people are actually actors. Fake rain starts pouring down and the actors run for the nearest shelter, in the same way as in the first scenario. However, here the individuals have a common goal (i.e. to get the scene shot), which interlocks their individual intentions (Bratman, 1992). The actions performed in these two scenarios are ostensibly identical, however, the context in which they occur distinguishes them in terms of the intentional relations between those involved.

In the present study we asked which processes are involved when observing individuals acting on shared intentions and when observing individuals acting on independent intentions that run in parallel. To that end we showed participants perceptually identical video clips depicting two people engaged in action. These

clips were ambiguous in terms of the intentionality of the people observed. We embedded the clips in varying contexts that were established by dialogues presented prior to the action videos. In one case the dialogue conveyed a shared intention where the actors agreed on doing something together (i.e. shared intention). In the other case, actors expressed independent individual intentions (i.e. parallel intentions). We compared the neural response to the action videos in the Shared Intention condition to the neural response to the Parallel Intentions condition. In the following we outline three specific aims.

Our first aim was to test whether observing actions performed with a shared intention engages different parts of the mentalizing network compared to observing the same actions performed without a shared intention. Mentalizing refers to the ability to reason about what others think, believe, wish or intend (Frith & Frith, 2010). Neuroimaging studies have isolated a neural network underpinning this ability. This network comprises the medial prefrontal cortex (MPFC), the superior temporal sulci and/or the temporo-parietal junction (STS/TPJ), the temporal poles and the posterior cingulate (PCC) and/or the precuneus (Gallagher & Frith, 2003; Schilbach, Wohlschlaeger, Kraemer, Newn & Shah et al., 2006). The MPFC is associated with representing mental states and with decoupling others' reality from one's own (Leslie, German & Polizzi, 2005). The STS/TPJ is thought to aid mentalizing by detecting agency in observed motions and also by supporting the holding of different perspectives (Gallagher & Frith, 2003; Frith & Frith, 2006). Temporal poles are associated with retrieval of semantic and episodic information that becomes useful in understanding others' mental states, particularly when they are socially engaged. The precuneus and the PCC have been attributed a more general role in relating to others' emotions (Ochsner, Knierim, Ludlow, Hanelin & Ramachandran et al, 2004) and mental states (Abraham, Werning, Rakoczy, von Cramon & Schubotz, 2008), as well as in self-referential processing (Saxe, Moran, Scholz & Gabrieli, 2006).

We know from previous research that the mentalizing network is at play when

people are immersed in online joint actions. Although some accounts (Saxe & Powell, 2006) argue that the TPJ, rather than the MPFC, is more specific to representing mental states, MPFC is more commonly found in mentalizing tasks that involve online interactions. In particular, MPFC activation is noted when participants play online interactive games with others, as long as they believe to be playing against another human and not a computer (Gallagher, Jack, Roepstorff & Frith, 2002; McCabe, Houser, Ryan & Trouard, 2011; Rilling, Sanfey, Aronson, Nystrom & Cohen, 2004; Rilling, Gutman, Zeh, Pagnoni, Berns et al., 2002). MPFC is also engaged when participants try to detect if someone is deceiving them, compared to when judging their beliefs (Grezes, Frith & Passingham, 2004). There is evidence to suggest that the mentalizing network also participates in observation of joint actions, for example when one needs to distinguish point-light displays of social interactions from two people acting independently (Centelles et al., 2011), or when inferring communicative intentions of the characters in static non-verbal cartoon stories (seen gesturing towards another character) compared to thinking about depictions of physical events (Walter, Adenzato, Ciaramidaro, Enrici, Pia et al., 2004; Ciaramidaro, Adenzato, Enrici, Erk & Pia et al., 2007). Together these findings suggest that this network, particularly the MPFC, is sensitive to others' social intentions, that is, when an individual's intention references the intention of another.

Accordingly, the first aim of the study was specifically to investigate if processing intentional relations, where the observed individuals' intentions are 'interlocked' (Bratman, 1992), involves mentalizing related computations. This should be manifest in differential activity in the mentalizing network when the observed individuals have a shared intention compared to when they act independently. Increased activation in the mentalizing network would imply that it does not only support attributing social intentions to single individuals but also supports the representation of interlocking intentions.

Our second aim was to determine whether similar processes are involved when

observers explicitly and implicitly keep track of intentional relations behind observed actions. There is behavioural evidence to suggest that mental or perceptual states of others are represented implicitly even when it is not required by the task (Kovacs, Teglas & Endress, 2010; Samson, Apperly, Braithwaite, Andrews & Bodley-Scott, 2010). We asked if intentional relations in the context of joint action are also processed involuntarily. To address this question we included two different tasks using the same stimuli (i.e. Intention task and Colour task). In the Intention task we asked participants to detect mismatches between the intentions the actors had expressed in the dialogue events and what they subsequently did. This makes an explicit demand on monitoring the intentions underlying the actions observed. In the Colour task participants were asked to detect a colour change in dots superimposed on the videos. This involved monitoring only perceptual features of the observed actions. If intentional relations are implicitly monitored even when it is irrelevant for task performance, then we should find the same neural areas to be recruited in both the Intention and the Colour tasks.

Finally, the third aim of the study was to determine whether observing joint actions based on shared intentions elicits a reward response in the observer, which would be reflected in activations in the reward-relevant neural network, particularly in the ventral striatum. Numerous studies have implicated this area when people are actively engaged in social interactions with others, for example when acting in synchrony (Miles, et al., 2009), engaging in direct eye gaze (Redcay, Dodell-Feder, Pearrow, Mavros & Kleiner et al., 2010; Schilbach, Wilms, Eickhoff, Romanzetti, Tepest et al., 2010) or when cooperating with others (Rilling et al., 2002; Rilling, Sanfey, Aronson, Nystrom & Cohen, 2004). It has been proposed that when we observe others, the experience we attribute to them is mapped onto our own prior experiences (Barresi & Moore, 1996). If a similar mechanism applies to observing interactions, then the same affective component of socializing with others should be resonated in the observer. This would be reflected in increased activation of the ventral striatum in the Shared Intention condition when compared with the Parallel Intentions condition.



## Method

### Participants

21 native speakers of Dutch (9 females; Mean age=22,  $SD=2.93$ ) participated in this study and received monetary compensation. From the 21, we excluded the data acquired from 5 participants from the analysis due to excessive head movements ( $>5\text{mm}$ ) or other technical difficulties at the time of data collection. All participants were right handed and had normal or corrected sight. The study was approved by the local ethics committee and complied with the Declaration of Helsinki.

### Stimuli and Design

Video clips of two people performing actions were embedded in varying contexts that framed the way the videos could be interpreted. Context was established by means of a dialogue that took place between the actors, which was presented prior to the action video. In the *Shared Intentions (SI)* condition, two people were heard to agree on doing something together (e.g. A: Shall we set the table? B: Yes good idea!). This was followed by the action video where two actors were engaged in action. In the *Parallel Intentions (PI)* condition the identical action video was preceded by a different dialogue, where actors express independent intentions (e.g. A: Shall we set the table? B: No I think I'll clean the cutlery). We included two tasks in the paradigm that were blocked. In both tasks the participants were instructed to count 'mismatch trials' within each block. In the mismatch trials of the Intention Task the content of the action video did not match the content of the dialogue video. In the Colour Task, the action videos that were presented in the Intention task were superimposed with two coloured dots that followed the actions of the actors. Here the task was to detect the trials where one of the dots changed colour.

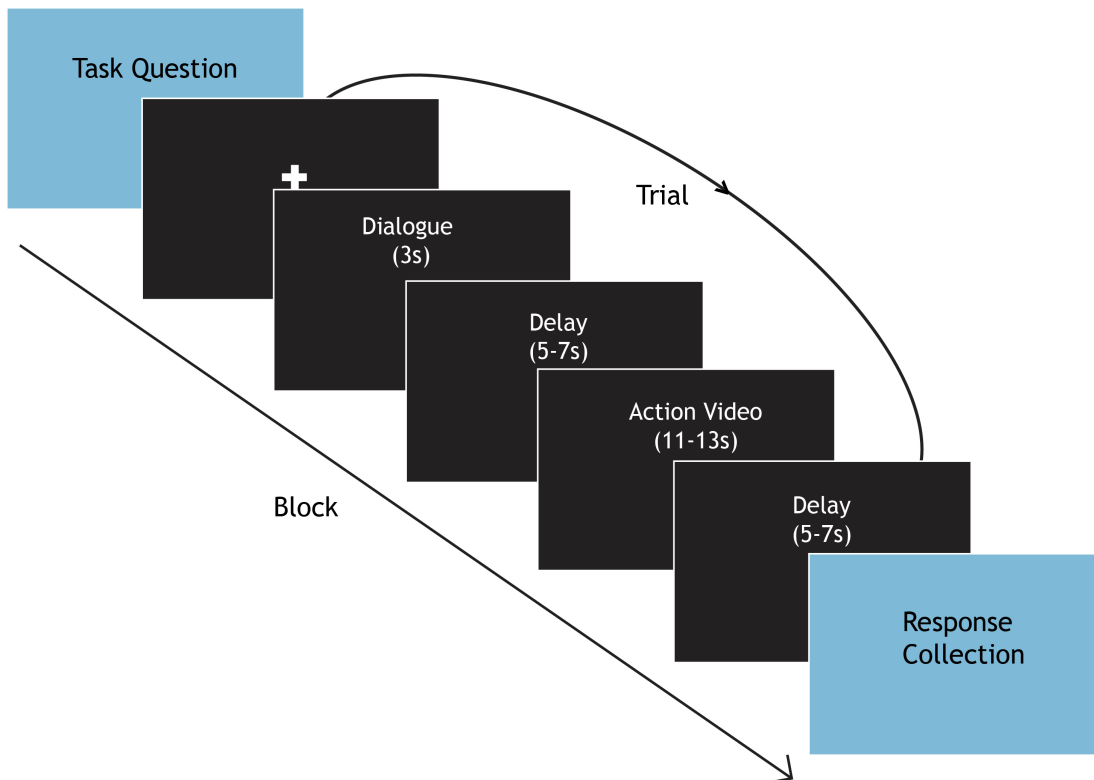
The stimuli consisted of two types of videos: dialogue videos and action videos. We recorded the videos in an actual apartment for natural scenery. In action videos, two different mixed-gender pairs acted out 5 different scenarios: cleaning the living room, setting the dining table, repairing the TV, folding the laundry, and making

coffee (see Appendix for details on scenarios). For example, in the cleaning scenario one of the actors sprayed cleaning liquid on a dining table and wiped it with a paper towel. The other actor, standing at the other end of the table, removed some books from a bookshelf located behind the actor and placed them on the table. The actors did not engage in eye contact during the videos, and no verbal or non-verbal communication took place. In the dialogue videos that were presented prior to the action videos, a still photograph of the room set-up was seen while the dialogue between the actors was overheard. In the Shared Intentions dialogue (SD), the actors agreed on cleaning the living room together. In the Parallel Intentions dialogue (PD) one actor expressed the intention to clean the living room, while the other expressed the intention to search for a book. Additional videos were recorded for mismatch trials (see Supplementary Materials for details). For example in the cleaning scenario, following the dialogue, the actors were seen playing cards in the same setting. We piloted the stimuli prior to the experiment. In a two choice task participants were asked after each trial (dialogue video + action video) whether the trial was a match or a mismatch. The difference in accuracy scores between mismatch and match trials was not significant (mismatch:  $M=96\%$ ,  $SD= 3.6$ , match:  $M=86\%$ ,  $SD=15.7$ ,  $t(4)=1.33$ ,  $p>.05$ ).

The same videos were further processed to create the stimuli used for the Colour task. The action videos were superimposed with two coloured dots, one placed on each actor. These dots followed the actions of the actors. For the mismatch trials in the Colour task one of the two dots changed colour at a particular time point. The average time the participants required to categorize each video as a match or a mismatch in the pilot study determined the time point for the colour change of the dot in the Colour task. All videos were processed using Adobe Premiere Pro CS4. The sound files in the dialogue videos were equalized using EQ Filtering 2.0 ([www.sens.com](http://www.sens.com)) software to correct for the distortion created by MRI signal.

## Procedure

Having provided informed consent, participants received instructions and were familiarized with the task in a short practice run before the scanning session. The practice task included different videos than the ones included in the experiment. The experiment consisted of 126 trials in total (see Supplementary Materials for details). The trial types (five scenarios, two actor pairs, and two actor locations) for each of the two tasks (Intention and Colour) were randomized across the experiment. In one such trial type Actor A started the dialogue and B responded, which was followed by the action video where A was seen on the left part of the screen and B on the right. In another trial type B started the dialogue and was seen on the left part of the screen in the subsequent action video.



**Figure 5.1:** Diagram illustrating the course of each trial.

Tasks were blocked, and blocks were presented in random order. Each block consisted of 10 (Colour task) or 11 trials (Intention task). Each trial (Figure 5.1) commenced with a fixation cross which was succeeded by the dialogue video that lasted for approximately 3 seconds. A jittered delay of 5-7s separated the dialogue event from the action event. The duration of the action events varied between 11 to 13 s depending on the scenario. This was followed by a jittered inter-trial interval (ITI; 5-7s). The task question was presented in the beginning of each block. For the Intention task the question was *“In how many of the following videos did the actors not do what they had agreed to do?”*, and for the Colour task the question was *“In how many of the following trials does one of the moving dots change colour?”*. At the end of the block participants were prompted to provide a response by choosing one of the given 4 options (0, 1, 2 or 3) via the button-box placed under their right hands. Stimuli were presented with Presentation® software ([www.neurobs.com](http://www.neurobs.com)).

#### Neuroimaging data acquisition

Participants lay in the scanner in supine position. Visual stimuli were presented on a computer screen outside of the scanner, which participants could see via mirror-glasses. Participants' heads rested within a 32-channel head array coil and was secured with pads and masking tape. T2-weighted echo-planar imaging blood-oxygenation-level-dependent (EPI-BOLD) fMRI measurements were acquired in 34 axial slices in ascending ordering (3 mm thickness, 0.5 mm slice gap) with a Siemens Trio 3T system using a 5 pulse multi-echo sequence (TE durations of 6.9, 16.2, 25, 35, 44 ms, TR=2.19 s, flip angle=80 deg, isotropic voxel size=3.5 mm). Following functional imaging T1-weighted images were obtained (TR=2.3 s, TE=3.03 ms).

#### Neuroimaging data analysis

The fMRI data were analyzed in an event-related manner within the general linear model, using SPM8 software (Wellcome Department of Imaging Neuroscience, London, UK) and Matlab R2007b (The MathWorks Inc., Natick, MA, USA). The 5 pulse multi-echo images were combined with an ad hoc Matlab script. Standard

spatial pre-processing (spatial realignment, slice-time correction, normalization to MNI space and spatial smoothing with a 6 mm Gaussian kernel (Friston, Holmes, Poline, Grasby & Williams et al., 1995) was performed. For the statistical analysis, the dialogue and action events were modeled as the events of interest for each condition. A jittered null event (5-7 s) placed between the dialogue and action events allowed the two events to be analyzed separately. 12 regressors were created for the six conditions (three action conditions x two tasks) with two events in each condition (dialogue and action). Mismatch trials were modeled as separate regressors and were not included in further analyses. All regressors were convolved with a canonical hemodynamic response function (HRF). To correct for motion-related artifacts, we modeled subject-specific realignment parameters as covariates of no interest. Linear contrasts of regression coefficients were computed at the individual subject level and then taken to a group-level random-effects analysis. The group analysis consisted of one-sample t-tests of the contrast images of all participants that indicated whether observed differences between conditions were significantly distinct from zero, or of paired t-tests of contrast images to analyze the statistical difference between. To protect against false-positive activations a double threshold was applied, by which only regions with a z score exceeding 2.94 ( $p < 0.005$ , uncorrected, and to  $p < 0.05$ , corrected) and a volume exceeding 60 contiguous voxels (corresponding to  $p < 0.05$ , corrected). This was determined in a Monte Carlo simulation using a Matlab script provided by Scott Slotnick (<http://www2.bc.edu/~slotnics/scripts.htm>).

## Results

### Behavioural results

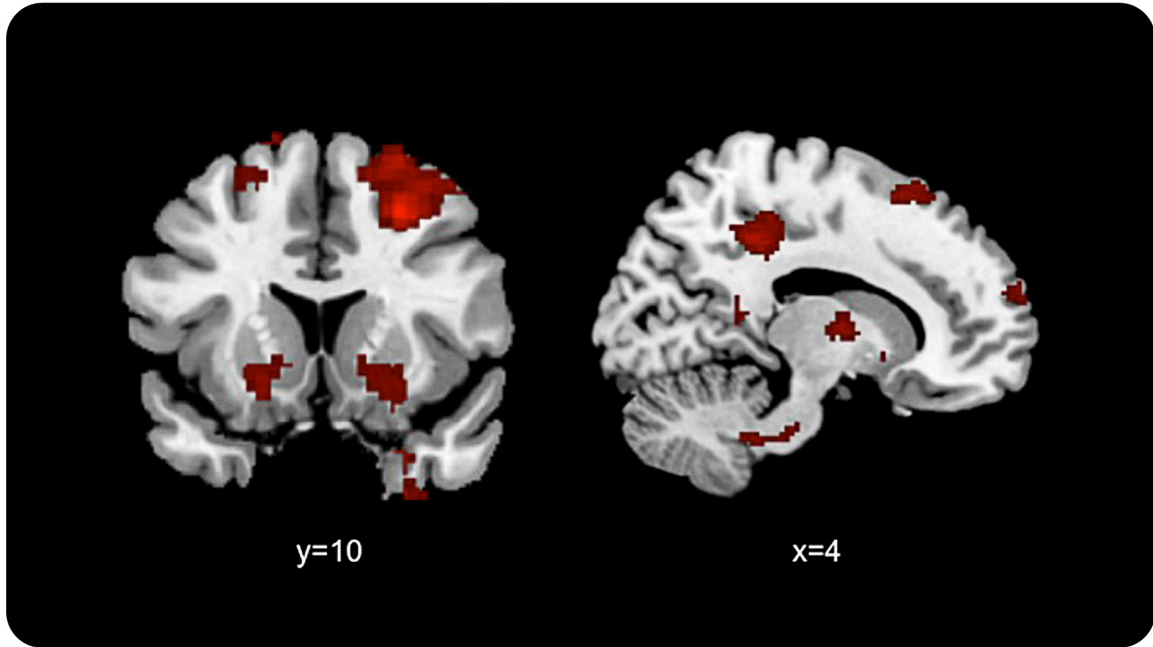
Due to a technical problem we were not able to acquire behavioural data from four out of 16 participants. The task was to count the number of mismatch trials within each block of trials. Participants correctly counted 71 of the 74 the mismatches in the Colour task (one sample t-test,  $t(11) = 0.737$ ,  $p > .05$ ). In the Intention task they overestimated the occurrence of mismatches (mean occurrence=74, mean reported

count=150, one sample t-test,  $t(11)=5.175$ ,  $p<.05$ ). Performance was thus better for the Colour task (paired samples t-test,  $t(11)=7.65$ ,  $p<.05$ ).

### Neuroimaging results

The primary question of this study was whether any neural regions would be more sensitive to shared intentions in observed social interactions than to multiple individual intentions when attending to intentions relative to when attending to perceptual events. To answer this question we first set out to investigate the main effects of the factors Intention and Task. When contrasting the Intention task against the Colour task ( $[SI_{\text{intention}}+PI_{\text{intention}}]>[SI_{\text{colour}}+PI_{\text{colour}}]$ ) we noted activations in the postcentral gyrus bilaterally, and the temporal pole in the right hemisphere (Table 5.1b). In the reverse contrast, activity in the bilateral middle occipital gyri, right fusiform gyrus, left superior parietal lobe, right middle frontal and right precentral gyri were noted (Table 5.1b). The main effect of Intention ( $[SI_{\text{intention}}+SI_{\text{colour}}]>[PI_{\text{intention}}+PI_{\text{colour}}]$ ) revealed significant activity in left middle and right superior occipital and right calcarine gyri (Table 5.1b). The contrast Parallel Intentions vs. Shared Intentions ( $[PI_{\text{intention}}+PI_{\text{colour}}]>[SI_{\text{intention}}+SI_{\text{colour}}]$ ) elicited no suprathreshold activations.

To explore the interaction between the factors Intention (Shared vs. Parallel) and Task (intention vs. colour) we carried out the following paired t-test: ( $[SI_{\text{intention}}>PI_{\text{intention}}] > [SI_{\text{colour}}>PI_{\text{colour}}]$ ). An interaction effect was associated with activation in the bilateral middle frontal gyri, left precentral and superior frontal gyri, posterior cingulate / precuneus, right temporal pole, nucleus accumbens bilaterally, right Heschl's gyrus, thalamus/caudate and the cerebellum (Table 5.1a, Figure 5.2).



**Figure 5.2:** Significant activations revealed by the paired t-test ( $[SI_{intention} > PI_{intention}] > [SI_{colour} > PI_{colour}]$ ) overlaid on a single subject T1 (voxel  $p < .005$ , cluster  $p < .05$ ).

To further scrutinize the interaction between the Intention and Task factors we carried out the following simple contrasts. The contrast between Shared Intentions and Parallel Intentions in the Intention task ( $SI_{intention} > PI_{intention}$ ) revealed activations in the rostral part of the anterior cingulate cortex (rACC) bilaterally, bilateral superior frontal gyri including pre/postcentral gyrus of the left hemisphere, middle cingulate gyrus and the precuneus, bilateral superior temporal gyri and medial parts of the temporal poles. Additional activations were found in midline thalamus, right caudate nucleus and right nucleus accumbens, and finally in the cerebellum (Table 1c). Conversely, when Parallel Intentions were contrasted with Shared Intentions ( $PI_{intention} > SI_{intention}$ ) no suprathreshold activations were observed. The contrast between Shared Intentions and Parallel Intentions events in the Colour task ( $SI_{colour} > PI_{colour}$ ) yielded no significant activations either.

**Table 5.1a:** Differential neural activations noted in the paired-test [ $SI_{intention} > PI_{intention}$ ] > [ $SI_{colour} > PI_{colour}$ ] to investigate the interaction between factors TASK x INTENTION (voxel level  $p < 0.005$ , and cluster corrected for multiple comparisons,  $p < 0.05$ , unless otherwise indicated).

Anatomical region		MNI coordinates			Cluster	Z
		x	y	z	size	
A. INTERACTION						
$[SI_{intention}>PI_{intention}] > [SI_{colour}>PI_{colour}]$						
Middle frontal gyrus	R	24	16	46	2869	4.78
Precentral sulcus	L	-32	-8	42	149	3.83
Superior frontal gyrus	L	-20	8	60	416	3.68
Middle frontal gyrus / Frontal Pole		-26	54	26	983	3.64
Precuneus/PCC	L	6	-38	46	723	4.12
Temporal pole	R	34	20	-36	189	3.96
Heschyl's gyrus	R	50	-16	4	75	3.17
Thalamus/caudate	R	8	-4	4	1010	3.64
	L	-16	-24	16	109	3.06
Nucleus accumbens	L	-18	10	-12	240	3.61
Nucleus accumbens/putamen	R	28	-8	4	<60	3.27
Cerebellum		0	-50	6	971	3.58
	R	16	-32	-38	109	3.06
	R	46	-52	-28	239	3.19
	L	-10	-34	-40	992	4.01



**Table 5.1b:** Differential neural activations noted in main effects (voxel level  $p < 0.005$ , and cluster corrected for multiple comparisons,  $p < 0.05$ , unless otherwise indicated).

Anatomical region		MNI coordinates			Cluster size	Z
		x	y	z		
<b><i>B. MAIN EFFECs</i></b>						
<b><i>I. Intention (SI&gt;PI)</i></b>						
Middle temporal gyrus	L	-52	-22	0	70	3.78
Superior occipital gyrus	R	24	-102	8	124	3.19
Middle occipital gyrus	L	-34	-80	2	65	3.17
<b><i>II. Intention (PI&gt;SI)</i></b>						
None						
<b><i>III. Task (Intention&gt;Colour)</i></b>						
Postcentral gyrus	R	48	-30	52	399	3.64
	L	-50	-24	46	71	2.95
Middle temporal pole	R	56	10	-34	61	3.17
<b><i>IV. Task (Colour&gt;Intention)</i></b>						
Middle occipital gyrus	L	-38	-72	14	1852	3.91
	R	30	78	18	118	4
Fusiform gyrus	R	28	-74	-8	93	3.16
Superior parietal lobule	L	-20	-58	52	173	3.26
Inferior frontal gyrus	R	48	18	6	502	3.7
Precentral gyrus	R	36	-2	48	320	3.58
Middle frontal gyrus	R	36	34	24	140	3.28

**Table 5.1c:** Differential neural activations noted in simple contrasts. (voxel level  $p < 0.005$ , and cluster corrected for multiple comparisons,  $p < 0.05$ , unless otherwise indicated).

Anatomical region		MNI coordinates			Cluster	Z
		x	y	z	size	
<b>C. SIMPLE CONTRASTS</b>						
<b>I. <math>SI_{intention} &gt; PI_{intention}</math></b>						
rACC	R	6	36	8	173	3.56
	L	-4	40	12	<60	3.01
Precuneus/PCC	L	-12	-38	36	288	3.36
Middle frontal gyrus	R	32	30	42	593	4.04
	L	-24	6	68	760	3.83
Frontal pole	L	-16	62	16	331	3.93
Postcentral gyrus	L	-32	-32	56	70	3.42
Temporal pole	L	-18	0	-34	152	3.41
	L	-20	-28	-14	72	3.32
	L	-18	0	-34	96	3.36
Superior temporal gyus	L	-50	-20	8	902	3.88
	R	52	-16	4	91	3.48
Putamen	R	26	10	-12	84	3.12
Caudate	R	24	2	16	376	3.61
Cerebellum	R	48	-52	-28	206	3.75
	R	22	-32	-28	472	3.71
	L	-14	-34	-32	627	3.89
<b>II. <math>PI_{intention} &gt; SI_{intention}</math></b>						
None						
<b>III. <math>SI_{colour} &gt; PI_{colour}</math></b>						
None						

## Discussion

We set out to investigate whether observing social interactions with shared intentions recruits different neural regions than observing social interactions with multiple independent intentions when attending to the intentions of those involved in the interactions compared to when attending to perceptual aspects of the stimuli. To that end, we compared the BOLD response evoked by observing perceptually identical yet intentionally ambiguous joint actions embedded in two different intentional contexts (i.e. Shared Intentions vs. Parallel Intentions) and in two different task settings (i.e. attend to intention vs. attend to colour). Our main contrast of interest was between the Shared Intention condition and the Parallel Intentions condition in the Intention task versus the Colour task ( $[SI_{\text{intention}} > PI_{\text{intention}}] > [SI_{\text{colour}} > PI_{\text{colour}}]$ ). This test revealed activations in the right temporal pole, precuneus/PCC (posterior cingulate), and bilaterally in the ventral striatum, as well as in the bilateral superior frontal gyri (SFG) and the left frontal pole. We focus on these results in the following.

### Mentalizing

Our first aim was to investigate whether processing intentional relations where the observed individuals' intentions are 'interlocked' (Bratman, 1992), involves mentalizing related computations. If shared intentionality in observed joint actions called upon processes involved in representing mental states of others', this should manifest itself in increased activations in the mentalizing network in the Shared Intention condition compared to the Parallel Intentions condition. Both the interaction analysis of the factors Intention and Task, and the simple contrast between Shared Intentions and Parallel Intentions conditions in the Intention task revealed activation in two areas of the mentalizing network, namely, the bilateral temporal poles and the precuneus/posterior cingulate (PCC). Other than participating in theory of mind reasoning, the precuneus/PCC seems to take on a more general role in social cognition. It is involved in self-awareness and self-related processing as well as when thinking about intentions of one's own

(Sommer, Dohnel, Sodian, Meinhardt & Thoermer, et al., 2007; den Ouden, Frith, Frith & Blakemore, 2005), or intentions of others' (Abraham et al., 2008). Activity in these regions are observed also when the task demands comprehension of cooperation or intentional deception as aspects of different intentional relations (Lissek, Peters, Fuchs, Witthaus & Nicolas et al. 2008). It is also involved in processing others' emotions (Saxe & Powell, 2006), as well as in self-awareness and self-related processing (Cavanna & Trimble, 2006).

The temporal poles have traditionally been implicated in the storage and retrieval of semantic information, and are thought to play a supporting role in mental state reasoning (Gallagher & Frith, 2003). They are found active both in complex offline (Funnell, 2001; Ross & Olson, 2010; Calarge, Andreasen & O'Leary, 2003; Abraham et al. 2008), as well as in online mentalizing tasks (Assaf, Kahn, Pearlson, Johnson & Yeshurun et al., 2009; Gallagher et al., 2002; Rilling et al., 2002; 2004) especially when the task involves a social story. Be it in the form of an online interaction, a written narrative or a comic strip, these tasks include a social script that captures conventions of conduct in particular situations. Social scripts are thought to aid processing of the social situations as they outline the behaviour of the interacting individuals in compliance with socially accepted practices. For example the script for dining at a restaurant entails the waiter seating the customers, bringing their order and ends with the customer paying the bill at the table. Patients with lesions of the temporal poles have been noted to struggle in acting according to these scripts (Funnell, 2001). Regarding the current study, we believe that the dialogues signaling an upcoming shared intentional interaction activated corresponding social scripts, reflected in the temporal pole activation. Social scripts are particularly relevant for social interactions where individuals act on a shared intention, as the interaction needs to follow certain rules of social conduct stipulated by the scripts (Gilbert, 2009). This is not so much the case when people act independently, which could explain the weaker response in the Parallel Intentions condition.

The interaction analysis did not result in differential signal in the other two regions that are commonly included in the theory-of-mind network. These areas are the temporo-parietal junction (TPJ) and the medial prefrontal cortex (MPFC). The respective roles of these two areas in ToM reasoning are still subject to debate in the field. Although the MPFC is commonly found in mentalizing tasks, including those that involve processing social interactions, it has been argued that the function of this area in mental state reasoning is not restricted to representation of mental states, but is more generalizable to processing social or emotional information of others (Saxe & Powell, 2006). Mental state representation, this account contends, is associated with TPJ activation. A study by Jenkins and Mitchell (2009) sought to differentiate two confounding aspects of commonly used ToM tasks: inferring intentions of others when the context is ambiguous, and representing different types of mental states (e.g. beliefs, intentions etc.). They found that while the latter process engages the TPJ, making sense of others behaviour when the situation is not sufficiently clear recruits the MPFC. Indeed, the tasks employed in the studies discussed in the introduction required participants to resolve ambiguities in the stimuli and found MPFC to be differentially involved when comparing social to non-social conditions (e.g. Walter et al., 2004; Ciaramidaro et al., 2007; Grezes et al., 2004; de Lange, Spronk, Willems, Toni & Bekkering, 2008). This was not the case in the current study. In the current study the information pertaining to the intentions of the observed individuals was made available to the participants via the dialogues before they observed the interactions. This explains the lack of MPFC activation in our results.

Whether processing mental states selectively recruits the TPJ (Saxe & Wexler, 2005; Jenkins & Mitchell, 2009), or the MPFC (Gallagher & Frith, 2003; Walter et al., 2004), the lack of activation in either of these areas in our results suggests that the brain is impartial to shared intentions and parallel intentions in observed social interactions with respect to the computations underpinning mental state representations. It has been proposed that the role of this computation is to decouple others' mental states apart from that of one's own (Leslie et al., 2005). Whether individuals act with a

shared intention or with independent parallel intentions, both cases comprise two agents with two respective intentions, which remain decoupled from one another. In both cases processing the intentional relation involves second-order theory of mind reasoning (Frith, 2007) to comparable extents in the two conditions. As Bratman argues (1992) what separates shared intentions from independent intentions is not their constitution, it is the way they are organized. Accordingly, shared intentions are ordinary intentions that are interlocked, processing which does not seem to burden neural areas associated with representing mental states.

#### Expectation of interlocked intentional actions

Are there other neural regions involved in computing interlocking of intentions in observed shared intentional actions? Two other regions that were found significant in the interaction analysis are possible candidates; the bilateral superior and middle frontal gyri and the frontal poles (Figure 5.2). Frontal poles have been implicated in integrating two or more separate cognitive operations in pursuit of higher goals (Ramnani & Owen, 2004), for example in multi-task coordination (Gilbert, Spengler, Simons, Steele & Lawrie et al., 2006), or in cooperative social interactions (McCabe et al., 2011). Superior frontal gyrus and the frontal poles have been associated with organization of sequential movements towards a desired final goal (Majdanzic, Grol, van Schie, Verhagen & Toni et al. 2007; van Schie & Bekkering, 2007). This suggests when perceiving joint actions, single actions of the partaking individuals are perceived as interlocking intermediary steps towards the attainment of the final goal. The activations we found in the SFG and the frontal pole in this contrast suggest that on the basis of the prior information provided with the dialogues people expect the upcoming observed action to be coordinated and interlocked in the Shared Intention condition. This may have lead them to monitor these actions as if they were indeed interlocked, even though they were perceptually identical to the actions in the Parallel Intentions condition. This implies a difference in processing of the otherwise identical stimuli. It is possible that the prior contextual information provided with the dialogues set the system to anticipate a certain contingency

between the actions of the observed individuals. The expected contingency could explain the activation also noted in cerebellum, an area known for its involvement in monitoring temporal aspects of movements (Schubotz, Friederici & von Cramon, 2000).

Is monitoring intentional relations implicit?

Recent behavioural evidence suggests that mental states of others can be computed implicitly (Samson et al., 2010; Kovacs et al., 2010). Our second aim was to test whether intentional relations in observed interactions are also processed implicitly. We addressed this question by including the Colour task, which was a perceptual task requiring participants to attend to the perceptual features of the stimuli. Monitoring the intentions behind the observed interactions was not relevant for this task. Therefore any mentalizing related activity found in this task ( $SI_{\text{colour}} > PI_{\text{colour}}$ ) would have indicated an implicit processing of intentional relations in the observed actions. However this contrast did not reveal any significant activation in the mentalizing network, or elsewhere, ruling out any differences in implicit processing between the contrasted conditions.

Reward processing

A further aim of the study was to determine if observing actions performed with shared intentionality triggers neural activity in reward areas in the onlookers. Indeed we found activation in the ventral striatum (nucleus accumbens), bilaterally. These areas (Izuma, Saito & Sadato, 2008) are involved in evaluation of social rewards (e.g. Delgado, Stenger & Fiez, 2004), such as money or reputation (Izuma et al., 2008; Elliott, Friston & Dolan, 2000). Just as in primary rewards, the reward circuitry mediates learning of contingencies between actions and their social rewards. Of particular interest, a number of neuroimaging studies detected activity in these areas when people were engaged in online social interactions where there is mutual contingency between the interacting individuals, compared to when individuals' actions are not contingent on one another (Walter, Abler, Ciaramidaro &

Erk, 2005; Behrens, Hunt, Woolrich & Rushworth, 2008). From minimal cases such as interpersonal gaze (Kuzmanovic, Georgescu, Eickoff, Shah & Bente et al., 2009; Redcay et al. 2010; Schilbach et al., 2010; Williams, Walter, Perra, Perrett & Whiten, 2005) or simple interactions such as playing ball with avatars (David, Bewernick, Cohen, Newen & Lux et al., 2006), to more complex ones that require reciprocal cooperative behaviour, for example in neuroeconomic trust games (Rilling et al., 2002), social interactions of a range of complexity call on these areas. This suggests that interacting with others where there is mutual contingency between individuals' behaviour generates a rewarding experience. What our findings suggest is that a similar response occurs when observing others in interaction, which possibly reflects a resonance with those observed and one's past experiences. To our knowledge, this is the first study to demonstrate that performing actions together based on shared intentions creates a rewarding experience not only in those who are engaged in the interaction, but also in those that are passively observing it.

What could be the reward value in observing interactions? We know that participating in social interactions is rewarding and facilitates subsequent cooperative and prosocial behaviours (Tomasello, Carpenter, Call, Behne & Moll, 2005). When observing others in interaction, the pleasant rewarding experience we attribute to those we observe might be mapped onto our own experiences that we previously acquired during our interactions (Barresi & Moore, 1996). Such a response might further reinforce our motivation to engage in shared experiences with others (Tomasello et al., 2005). It may also serve as a means to learn information that is not available when observing others in isolation, thereby facilitating cultural transmission of joint practices.

As a final note, the simple contrast between Shared Intentions and Parallel Intentions in the Intention task ( $SI_{\text{intention}} > PI_{\text{intention}}$ ) revealed a very similar pattern of activation as observed in the main contrast reported in the above. However, no suprathreshold activity was detected in the opposite contrast ( $PI_{\text{intention}} > SI_{\text{intention}}$ ). In all, this unidirectional difference in the neural response we find between Shared



Intention and Parallel Intentions conditions when the task was to attend to intentions, suggests that observing social interactions with shared intentions has increased processing demands compared to observing individuals who act independently. This relative demand seems to be related to the (explicit) tracking of interlocking intentions, which involves social cognitive processes. Observing shared intentional interactions seem to recruit social script knowledge, which in turn might bias how the unfolding of the interaction is perceptually monitored. Finally, our data suggest that the rewarding experience elicited in individuals who are socially engaged in interactions (Schilbach et al., 2010) spreads to others who observe them.

## Supplementary Materials

### Stimuli

The experiment consisted of 126 trials in total, equally distributed across the three conditions (Shared Intention, Parallel Intentions, Individual Intention). The Colour task comprised 60 trials. 6 of those trials were randomly picked and modified as a mismatch trial, in which one of the two superimposed dots changed colour. The Intention task comprised 66 trials. The extra six trials included action videos that had a different content than any of the five scenarios. We did not include these content-wise mismatches in the Colour task, because adding a colour change on them would create a mismatch in two dimensions: content and colour.

### Individual Intention Condition

A third condition was included in the experiment that involved an individual intention (*II*). Here, the dialogue portrayed only one actor expressing an intention (e.g. A: What are you going to do? B: I think I'll clean the cutlery). The action video that followed only one of the actors engaged in an action and was passively observed by the other.

The data analysis of the contrast between Shared Intentions and Individual Intention conditions in the Intention task ( $SI_{intention} > II_{intention}$ ) revealed significant activations in bilateral occipital cortices, bilateral superior temporal gyri, overlapping with auditory cortices and flowing posteriorly towards the temporo-parietal junction, bilateral pre/post central sulci as well as the left frontal eye field, left frontal pole, precuneus and the left superior parietal lobule. Parallel actions, when contrasted with individual actions in the intention task ( $PI_{intention} > II_{intention}$ ) recruited the occipital cortices and the superior temporal gyri bilaterally (Supplementary Table 5.1).

**Supplementary Table 5.1.** Differential neural activations noted in simple contrasts: I. Shared Intentions and Individual Intention in the Intention task, and II. Parallel Intentions and Individual Intention in the Intention task (voxel level  $p < 0.005$ , and cluster corrected for multiple comparisons,  $p < 0.05$ ).

Anatomical region		MNI coordinates			Cluster size	Z
		x	y	z		
<b><i>I. <math>SI_{intention} &gt; II_{intention}</math></i></b>						
Heschl's gyrus	R	58	-20	6	2096	4.92
	L	-50	-2	6	2442	4.73
Middle frontal gyrus	L	-36	16	52	546	3.88
	L	-26	56	8	259	3.25
Postcentral gyrus	R	42	20	48	92	3.16
	R	38	60	10	64	3.22
	L	-28	-4	62	130	3.32
	R	56	-24	56	239	3.29
	R	8	-44	68	209	3.15
	L	-30	-5	60	66	2.79
Superior fontal gyrus	L	-10	28	60	134	3.19
Precuneus	R	10	-44	12	222	3.24
Cuneus	R	10	-94	14	7904	4.72
Cerebellum	R	48	-60	26	220	3.26
<b><i>II. <math>PI_{intention} &gt; II_{intention}</math></i></b>						
Cuneus	R	20	-96	18	1890	4.7
	L	-30	-76	-2	1718	4.54
Heschl's gyrus	R	58	-20	6	203	3.31
	L	-50	-2	4	161	3.13
Middle frontal gyrus	L	-38	14	48	100	3.06
Cerebellum	L	-44	-74	-20	82	3.04

## Appendix

Stimulus scenarios that describe various activities of the actors in the stimuli.

### 1. Cleaning

#### *Dialogues:*

Shared Intention: A: Shall we clean the living room? B: Yes good idea!

Parallel Intention: A: Shall we clean the living room? B: No, I think I am going to look for my book.

Individual Intention: A: What are you going to do? B: I think I will clean the living room.

#### *Action Videos:*

Shared/Parallel Intention: A sprays cleaning liquid on the table and wipes it with a paper towel. B is standing up across the other end of the table and takes some books out of the bookshelf behind and places them on the table.

Individual Intention: A wipes the table in the same way as in the Shared/Parallel Intention videos, while B is standing up across the other end table and watches A.

### 2. Repairing

#### *Dialogues:*

Shared Intention: A: Shall we repair the TV? B: Yes good idea!

Parallel Intention: A: Shall we repair the TV? B: No, I think I will repair the door.

Individual Intention: A: What are you going to do? B: I think I will repair the TV.

#### *Action Videos:*

Shared./Parallel Intention: A is sitting on the sofa next to the TV, and presses the switch button on it and then tries the remote control. B is standing across A by the door and takes a screwdriver out of the toolbox.

Individual Intention: A is attending to the TV and the remote control in the same way as in the Shared/Parallel Intention videos while B is standing and watching A.

### 3. Table setting

#### *Dialogues:*

Shared Intention: A: Shall we set the table? B: Yes good idea!

Parallel Intention: A: Shall we set the table? B: No, I think I will clean the cutlery.

Individual Intention: A: What are you going to do? B: I think I will set the table.

#### *Action Videos:*

Shared/Parallel Intention: A is placing place mats on the table. B is sitting across the table and wipes the cutlery on the table with a kitchen towel.

Individual Intention: A is placing place mats on the table. B is sitting across and watching A.

### 4. Folding

#### *Dialogues:*

Shared Intention: A: Shall we do the laundry? B: Yes good idea!

Parallel Intention: A: Shall we do the laundry? B: No, I think I will pack my suitcase.

Individual Intention: A: What are you going to do? B: I think I will do the laundry.

#### *Action Videos:*

Shared/Parallel Intention: A is sitting on one end of the bed and folding some clothes. B is sitting on the other of the end next to a small suitcase places on the bed, and also folds some clothes.

Individual Intention: A is sitting on one end of the bed and folding some clothes. B is sitting on the other end of the bed and watches A.

### 5. Coffee making

#### *Dialogues:*

Shared Intention: A: Shall we make coffee? B: Yes good idea!

Parallel Intention: A: Shall we make coffee? B: No, I think I'll have some yogurt.

Individual Intention: A: What are you going to do? B: I think I'll make coffee.

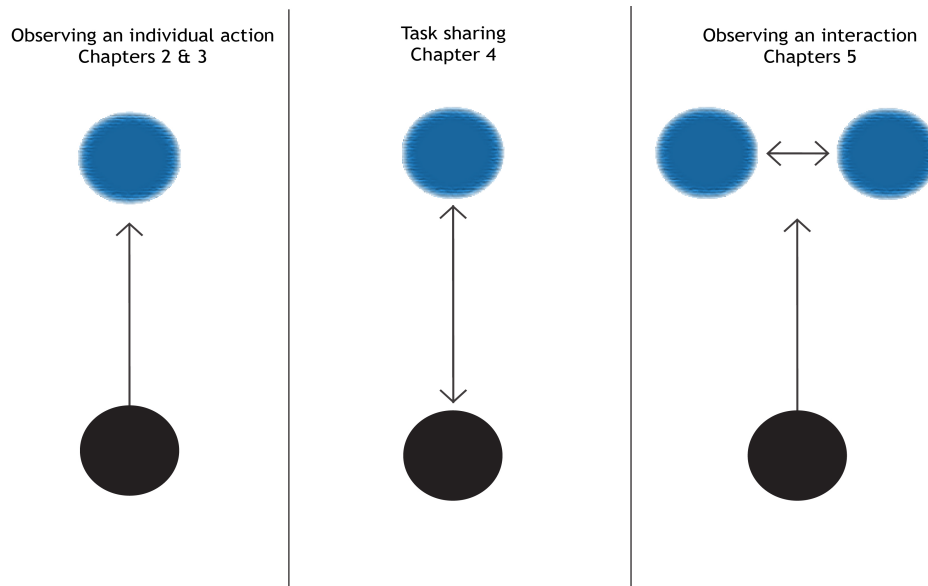
#### *Action Videos:*

Shared/Parallel Intention: A is filling the kettle with water from the tap, and turning it on. B is next to A, taking the milk carton from the fridge.

## Chapter 6

# Summary & General Discussion

Navigating the social world relies on our capacity of explaining and anticipating what others are doing. Whether we passively observe a dancer in the park or listen to a defense attorney at a hearing, we are in demand of social perception processes in order to understand others' behaviour. This thesis aimed to explore the workings of social perception as a mediator between individual cognitive processes and the requirements of social interaction. Four studies investigated the ways in which low level processes, supporting action perception, are exploited and constrained by processes that operate at higher levels, such as mentalizing, in understanding and explaining what others will do. Three different social contexts or social interactions have been employed (Figure 6.1): observation of an individual's actions, a social interaction where two individuals jointly perform a task, and finally observation of a social interaction that takes place between others. I summarize below the main findings of the thesis. Subsequent to that is a three-part discussion that examines the implications of the studies followed by concluding remarks.



**Figure 6.1:** The different social contexts addressed in this thesis. Black circles represent the observing agent (the participant), blue circles represent the observed agents.

## Summary

**Chapters 2 and 3** were concerned with the role of perception action matching and motor simulation in observation of individual actions and specifically addressed the following questions: (a) Does the basic principle of speed-accuracy trade-off in motor control constrain action simulation? (b) What is the role of the motor regions in calculation of the speed-accuracy tradeoff in observed actions? In two studies an observation version of Fitts' task was adopted. Participants were asked to judge the feasibility of an observed repetitive movement between two identically sized targets that were varied in size and placed at varying distances. According to Fitts' law (Fitts, 1954), a fixed relation between the size of the targets and the distance separating them (movement amplitude) indexes the difficulty of a particular movement and determines the time required to complete it.

The study reported in **Chapter 2** specifically investigated whether and how a selective impairment in the execution of an action would be present when the same action is perceived. A neuropsychological patient who suffers from a lesion in his left motor cortex presented in his action execution a particular violation of Fitts' law. When performing the Fitts' task—alternating a finger between the targets without missing them—the movement times scaled with the movement amplitude, instead of the index of difficulty. Likewise, when asked to judge the feasibility of the same repetitive movement performed by an observed actor, his judgments again changed as a function of the movement amplitude. In both cases of production and perception of the movement the patient exhibited a specific deficiency in integrating the target size into his motor representations. Due to neural damage, the patient's motor system seemed to fail at computing all the relevant information for production of a movement, and thereby failing to fully inform his motor simulations of the same action that is observed.

**Chapter 3** presented a functional neuroimaging (fMRI) study conducted with healthy adults. In a similar action perception paradigm as described in Chapter 2, the motor difficulty of the observed movements was systematically manipulated



while controlling for perceptual features. The results revealed an increase in neural signal in response to increasing levels of motor difficulty in the observed movements in brain regions that are involved in motor production. These regions include the primary motor cortex (M1), supplementary motor area (SMA) and the globus pallidus of the basal ganglia (BG). Crucially, perceptual aspects of the observed movements (i.e. varying levels of target size and movement amplitude) did not yield any signal change in these regions. Particularly interesting in the data is the lack of any activation in the human mirror system (i.e. inferior parietal lobule, IPL, prefrontal cortex, PFC, and the superior temporal sulcus, STS) (Rizzolatti & Sinigaglia, 2010). Research on mirroring mechanism in humans suggests that this neural circuitry is particularly sensitive to the degree of overlap between the observed actions and the corresponding motor representations. Such overlap is reflected in the intensity of the neural signal notes in these regions. In this study, however, the manipulation targeted a specifically motor parameter, the difficulty of the observed movement. Therefore, differential activation noted in the reported motor regions reflects a modulation in the system once a perception action match has been established.

**Chapter 4** addressed the modulating effects of representing another's goal on individual processing during an ongoing social interaction. Particularly, two experiments investigated whether and how representing another's task during a joint task performance would result in diffusion of information across agents during memory encoding. Two individuals performed a word categorization task that was distributed between them. They responded to the words of their individually assigned categories. They performed the task once alone and once together with their partners, and were later on tested for their memory in a surprise free recall protocol. The results of the first experiment demonstrated that individuals involuntarily remembered items belonging to their partners even though it was not relevant for their individual performance. The second experiment presented participants with a monetary incentive to encode items belonging to their assigned word categories. In the cued recall protocol they were asked to remember items

from all categories. The results confirmed the findings of the first experiment, and further demonstrated that remembering items that are irrelevant for one's individual task does not tax performance.

**Chapter 5** was concerned with ascription of shared intentions to observed interactions. An fMRI study that asked whether processing of social interactions that are driven by shared intentions recruits different neural computations than the processing of independent actions of multiple individuals. In an observation paradigm, perceptually identical actions carried out by two actors were presented in different intentional contexts that defined whether actors were going to perform a joint action or not. A dialogue that took place between the actors was heard beforehand that described the intentional relations (i.e. shared intention vs. parallel independent intentions) involved in the upcoming interaction. The results revealed that when compared to observation of interactions based on parallel intentions, observation of interactions based on shared intentions elicited increased activation in areas that include the temporal poles, the precuneus, and the ventral striatum. Precuneus and the temporal poles have been implicated in mentalizing, the latter with a more specific role in retrieving memories associated with social scripts. Thus mentalizing related computations also play an important role in identifying social interactions. The noted activation in the ventral striatum, with its well established involvement in processing primary as well as social rewards, might be indicative of a rewarding experience in the observer induced by observation of social interactions that are based on shared intentions.

## **General Discussion**

### **Observing individual actions and the role of motor simulations**

When we observe a movement by somebody else our motor system activates a corresponding representation that we use in executing the same movement. As postulated by action perception theories, common coding of perceived and

executable actions (Prinz, 1997) allows for motor simulations harnessing the observer's internal models that are essential for production of movements (Wilson & Knoblich, 2005). A system that utilizes production mechanisms in perception of movements renders action perception, largely a motor process. Both studies presented in Chapters 2 and 3 provide strong support for this theory. The neuropsychological case study reported in Chapter 2 provides a clear demonstration of how it is through the models that reside in the motor system that we get to process the actions we observe. The studied patient's processing of movements mirrored a particular impairment in the internal models that was likely caused by neural damage in his brain. The findings of the neuroimaging study in the subsequent chapter are more distinct. In this study, the motor system was found to specifically respond to a motor parameter (i.e. difficulty) of the observed actions. This suggests that once the corresponding action representations get activated, motor system codes the parameters that are not perceptual but purely motor, implying that action perception process involves more than just recognizing actions, and recruits neural regions beyond the mirror system. The involvement of the motor system in perception could provide the observer with information that is motor-specific. To illustrate, going back to our kitchen scenario, when my friend lifts the heavy pot filled with water my motor system doesn't only recognize the action as lifting, but it also identifies the effort she applies. This is consistent with previous behavioural work that has shown how this information leaks into the autonomic system and modulates the observer's heart rate and respiration (Mulder, de Vries & Zijlstra, 2005; Decety, Jeannerod, Durozard & Baverel, 1993).

What kind of advantages does such intimate motor knowledge offer? Motor simulations deliver fine-grained predictions with respect to the perceptual consequences of another's action and in real-time (Wilson & Knoblich, 2005). Such anticipated effects serve to inform individuals' action plans and allow them to make the necessary adjustments in performance. For example, when my friend raises her hand in anger (because I dropped the sugar packet and we're covered in caster sugar) owing to my proficiency in predicting exactly when and where her hand is

going to land I can duck down at the right moment to save my face. Thanks to my motor system that computes the force involved I can also anticipate the pain the slap would cause me. An interesting question is whether and how simulating the effort involved in an observed action might relate to empathic responses. Would an observer simulate the pain that is associated by exertion in the absence of perceptual information about emotional expressions of the observed person?

What other information can individuals derive about the observed actions by simulating them? An ongoing debate that initially started with the discovery of mirror neurons has been on the role of action matching in understanding the intentions of observed actions. One account asserts that through the direct matching process that activates the mirror system we can understand actions (Rizzolatti & Sinigaglia, 2010; Gallese, Rochat, Cossu & Sinigaglia, 2009). The opposing account argues that understanding is an inferential process that involves functional and neural computations that are beyond mirroring (Gergely, 2007). Recent evidence supports the latter. The most likely reasons behind actions can be computed by direct matching through integrating the observed kinematics and the contextual cues to generate predictions that are continuously tested as the action unfolds until a hypothesis is confirmed (Kilner, Friston & Frith, 2007; Rizzolatti & Sinigaglia, 2010; Iacoboni, Molnar-Szakacs, Gallese, Buccino & Mazziotta et al., 2005). However, when the actions appear 'implausible' given particular contextual cues, neural regions associated with mentalizing are recruited (Brass, Schmitt, Spengler & Gergely, 2007; de Lange et al., 2008; Wheatley, Millville & Marvin, 2007).

These findings imply that understanding observed behaviour involves a complementary interaction between the functional and neural mechanisms that subserve mirroring and those that subserve mentalizing. This might entail attaching the activated motor representation, which is thought to be agent-neutral (Frith, 2007), to an agent. In line with this reasoning, a particular computation that is thought to underpin mentalizing is the decoupling of perspectival states of the observer and the target agent, which differentiates the self from the other (Decety &

Sommerville, 2003; Ruby & Decety, 2001; Roepstorff & Frith, 2004). Self-other differentiation is important not only when a bottom-up inference is required to ascribe likely intentions to observed actors. It becomes especially critical in social interactions where one has to inhibit the mirroring activation in selection of an appropriate course of action. The next part of the thesis addressed social interactions with a focus on the ways in which automatic sensorimotor mechanisms and higher level thought processes reciprocally influence each other to optimize predictions in support of the social interaction.

### **Task sharing and memory encoding**

The study described in Chapter 4 examined a participatory case of social perception, addressing the particular question of how representing another's goal can modulate individual cognitive processes during an ongoing interaction. The particular context captured is a common case of interaction between two people who perform a task alongside one another. Previous work on task sharing has shown that when people perform two independent halves of a task they form representations that detail not only their own part of the task, but also the part of their interaction partner's (e.g. Sebanz et al., 2003; 2005; Atmaca et al., 2011). Individuals take into account the specific features of a stimulus that require the other to act upon, as well as their visuo-spatial perspectives (Boeckler et al., 2011; Samson et al., 2010) or attentional relations with the stimuli (Boeckler, et al., 2012). This, in turn, influences a range of online processes including prediction and monitoring during the ensuing interaction (Ramnani & Miall, 2003, Schuh & Tipper, 2007; de Bruijn et al., 2009), and stimulus processing. The study in Chapter 4 demonstrated that representing a co-actor's task also influences processes of memory encoding. Information that was strictly relevant for the co-actor was encoded even though it was not relevant for the purposes of one's own task performance.

These findings contribute to the understanding of social influences on memory. Research on collaborative memory (e.g. Basden et al., 2000; Rajaram & Pereira-Passarín, 2007; Weldon & Belringer, 1997, Basden, Basden & Henry, 2000) and

memory conformity (Wright & Schwartz, 2010) has demonstrated how remembering information together with others reshapes memories. The study reported in Chapter 4, by manipulating the social context during encoding of information, demonstrated that effects of social interaction on memory are not restricted to retrieval, but also influence encoding. Most importantly, it showed that even when individuals do not need to pay attention to each other's stimuli, a co-actor can affect memory performance. This suggests that social effects of memory can occur even when people do not have the shared goal to retrieve or encode information together. An intriguing question is how would the results change had the individuals been asked to perform together? Research on transactive memory (Wegner, 1986; Wegner et al., 1991) shows that when individuals act as a pair with a common goal to learn a material together, they distribute the material across the individuals as a strategy to maximize resources and recall performance. Would task-sharing individuals still encode their co-actor's information in a cooperative context, or would they be able to inhibit this involuntary mechanism for the sake of the group? This hypothesis has yet to be tested.

The findings of the study also add to the previous work on co-representation by demonstrating that co-representation effects are not restricted to online processes. As revealed by two experiments, individuals recalled the stimuli that required an interaction partner to act better than the stimuli that required nobody to act. This suggests that, representing the co-actors task rendered information relevant for them also relevant for oneself and enhanced encoding of the information, even though this was unnecessary for one's performance of the task. Surprisingly, processing the co-actor's information did not come at a cost to individuals' own memory performance. As clearly demonstrated in Experiment 2, even though the monetary incentive motivated individuals to allocate all resources to learning of their own stimuli, the recall rate for other-relevant information remained the same with that in Experiment 1. This indicates not only that individuals could not help but learn each other's information, but also it did not tax their memory processing of the stimuli.

This finding seems to conflict with the previous findings in task-sharing studies, where co-representation was found to interfere with individual processing and to result in a slowing down of reaction times. Although the exact mechanisms underlying this effect are not yet fully understood, a recent account compellingly suggests that self-other discrimination could be a potential answer (Wenke et al., 2011). Representing a co-actor as another agent with a perspective (visual or mental) different from one's own is likely to be resource consuming when the stimulus or the required response presents a conflict that one has to resolve. In particular, costs will occur when one needs to juxtapose two perspectival states (of self and of the other) in order to resolve a present conflict in selecting the appropriate course of action (Samson et al. 2010, Qureishi, Apperly & Samson, 2010). If this need is not present we can spontaneously and efficiently compute others' visuo-spatial perspectives (Samson et al., 2010) and belief-like states (Kovacs et al., 2010). In the experiments reported in Chapter 4 of this thesis, when responding to the stimuli, there was no need to resolve a conflict to interfere with individual processing and therefore, no need to decouple self from the other. Thus, just as in the case of computing perspectives and belief-like states, individuals may have implicitly coded the information that was relevant for another, and this may have enhanced the encoding processes.

In summary, this study has contributed to joint action research by demonstrating that when individuals act together to perform different parts of a task, they cannot help but encode the information their partner is processing. In general, co-representation mechanisms serve individuals by constraining the predictions they generate whilst trying to interpret other people's behaviour (Ramnani & Miall, 2003). Knowing in advance what the other is intending to do prevents one's predictions from running wild with infinite degrees of freedom, thereby aiding understanding. Co-representation can also aid social interactions, albeit indirectly. Representing another's task, how they relate to the information in terms of what they intend to do (e.g. Sebanz et al., 2003; 2005), or how they perceive it (Boeckler et al. 2012) provide a common ground between individuals as a foundation for

understanding each other's behaviour (Clark, 1996; Garrod & Pickering, 2004; Sebanz et al., 2006b) thus facilitating the progression of social interactions. The findings of the study demonstrate that acting together can be a means to maintain such a common ground because remembering information that is relevant for an interaction partner can contribute to the formation of shared knowledge systems (Shteynberg, 2010).

### **Observing social interactions and ascribed shared intentionality**

The third and the final section of the thesis brought into focus the processes underlying observation of social interactions that take place between other individuals. The available findings suggest that, much like the sensitivity we have for others' actions and intentions, we have a similar sensitivity towards other people's intentions in relation to one another. For example, we detect contingencies between the movement trajectories of different arbitrary objects (for a review see Scholl & Tremoulet, 2000) and attribute elaborate mental states to them (Schultz, Imamizu, Kawato & Frith, 2004; Schultz, Friston, O'Doherty, Wolpert & Frith, 2005). Perceived contingency can elicit in the observer a tendency to ascribe intentions to the objects that relate them to each other (Lakens, 2010; Lakens & Stel, 2011; Ip, Chiu & Wan, 2006). In particular, we tend to think that if agents move together, they must be moving with a shared intention to do so (Ip et al., 2006). To corroborate this finding recent studies have shown that observing contingent actions performed by two individuals elicits neural activity in regions that are associated with mental state reasoning (i.e. medial prefrontal cortex, MPFC) (<sup>1</sup>, Centelles et al., 2011).

The findings sketched above indicate that we have a propensity to detect relations between agents and perceive them as a unit that acts with a goal common to the involved agents. This could imply that much like the intentional stance we adopt when observing individual agents, we may well have a tendency to take an 'intentional stance' (Dennett, 1996) when observing a group of people who appear

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<sup>1</sup> Unpublished data collected in collaboration with Cordula Vesper, Janeen Loehr and Floris de Lange. Manuscript is in preparation.



to be socially engaged (Pettit, 2009). The intentional stance is thought to serve as an interpretive heuristic in explaining behaviour by establishing a set of predictions with respect to how that behaviour should ensue. Such a heuristic could also be applied to social interactions of other people. Then, a top-down modulation should be expected in processing the sensory features of the observed interaction. The results found in the study described in Chapter 5 support this hypothesis. This study specifically asked how advance knowledge pertaining to the intentional relations between interacting individuals (shared intentions compared to multiple parallel intentions) would exploit and constrain neural processing of the observed interaction. The differential neural response noted in lateral frontal regions (i.e. middle and superior frontal gyri, and the frontal pole) suggest that observed interactions that are based on a shared intention may be perceived as more interdependent than observed interactions that comprise multiple individual intentions. Thus, it could be argued that the ascribed intentional relation created a set of expectations in the observer, which manipulated how the actions of two people were perceived. Further behavioural and neuroimaging studies are required to scrutinize this interpretation and to specifically test if the action streams of interacting individuals are perceived as interlocked and hierarchically organized.

The results are particularly significant in terms of the underlying processes associated with mental state reasoning. When interacting with others, representations that are related to ‘self’, and representations that are related to ‘other’ need to remain differentiated in order for the interaction to progress. However, in particular cases of social interaction where individuals have a shared intention to achieve a certain goal, a group level representation may emerge. For example, back in the kitchen *we* (my friend and I) are making Turkish delight. Or, *they* (the English national football team) are playing against Portugal. Attributing a unified ‘they’ intention in addition to attributing individual intentions to the observed individuals could impose a higher load on mental state processes that are recruited when observing an interaction that involves a shared intention. However, the results of the current study do not support this hypothesis. A differential signal

change in the MPFC was not noted during the observation of interactions based on a shared intention compared to the observation of multiple independent actions, suggesting a lack of difference in terms of the neural computations underlying mental state representations. MPFC has been implicated in theory-of-mind processing as supporting the decoupling of perspectival states of individuals (Gallagher & Frith, 2003; Frith, 2007). Accordingly, the lack of differential activity in this region implies that in both social instances the observed individuals are represented separately with their respective mental states, whether their actions are interlocked or not.

A further finding was that observing interactions based on shared intentions evoked increased activation in the nucleus accumbens, bilaterally. Extending on previous neuroimaging studies that detected activity in these areas when people were engaged in online social interactions (such as in cooperation, e.g. Rilling et al., 2002, McCabe et al., 2011), the findings suggest that observing others perform joint actions may be as rewarding as being engaged in performing a joint action with others. As argued in the previous chapter, this possibly reflects a resonance with those observed and one's past experiences. To our knowledge, this is the first study to demonstrate that performing actions together based on shared intentions creates a rewarding experience not only in those who are engaged in the interaction, but also in those that are passively observing it. This raises the question of why this would be the case? What could be the reward value in observing social interactions? Perhaps the rewarding experience we attribute to those we observe are mapped onto our own experiences that we have previously acquired during our first hand social interactions (Barresi & Moore, 1996). Such a response might further reinforce our motivation to engage in shared experiences with others (Tomasello et al., 2005), and facilitate subsequent prosocial behaviours (Tomasello, Carpenter, Call, Behne & Moll, 2005). It may also serve as a means to learn information that is not available when observing others in isolation, thereby facilitating cultural transmission of joint practices.

## **Conclusion**

As humans, we are inherently tuned in with others. Owing to our acute sensitivity towards others' actions, perceptual or mental perspectives, and interactions with other people, we are able to explain their behaviour with remarkable ease. There are many processes that offer us access into the minds of others, and different aspects of social interactions can invoke them. This thesis reported investigations of three such mechanisms of social perceptions in different social contexts. Action perception coupling and motor simulation mechanisms allow one to automatically track and process the actions of another person by producing finely specified predictions into the future of the observed actions (Chapter 2, 3). Shared task representations that arise when performing a task jointly with another person, provide a means to implicitly track and process the goals of that person. Shared task representations also modulate the processing of the information that others are encoding (Chapter 4). Finally, when observing social interactions taking place between other people, explicit mentalizing processes allow us to attribute intentions and intentional states to the observed individuals. This in turn can modulate action perception processes (Chapter 5).

Understanding the mechanisms of social perception is key to understanding what is unique in the way humans cooperate. Cooperation in essence is interlocking of individuals' actions, goals and intentions. It is eventuated by the negotiations that take place between the individual cognitive mechanisms and the demands of social interactions that are situated in an infinitely complex social world. If there is one vital component for such negotiations to so much as launch, it is the proficiency with which individuals can justify and predict other people's behaviour. Research on Social Cognition and Social Neuroscience has accumulated a wealth of insight in understanding how we do this. So far, the investigations have focused on the 'other' as an individual. Investigating how we read the behaviour of the 'others' as a collective would be a worthwhile next step in the endeavor.

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## Nederlandse Samenvatting

De vraag die in dit proefschrift centraal staat, is hoe individuele cognitieve en neurale processen waarneming en begrip van het gedrag van een iemand anders ondersteunen. In vier hoofdstukken wordt verslag gedaan van vier studies naar processen van sociale perceptie, gebruikmakend van drie verschillende vormen van sociale interactie of sociale context, namelijk het observeren van de acties van een individu (hoofdstukken 2 en 3), het interacteren met een ander individu om samen een taak uit te voeren (hoofdstuk 4), en het observeren van sociale interactie (hoofdstuk 5).

**Hoofdstukken 2 en 3** gaan over de vraag of individuele motorische processen en de daarbij behorende neurale processen bijdragen aan de perceptie van de acties van een ander individu. In twee studies werd een observatie versie van Fitts' taak gebruikt. Proefpersonen werden gevraagd een geobserveerde herhaalde beweging tussen twee identiek grote doelen te beoordelen. De grootte en de afstand tussen de twee doelen werd gemanipuleerd. Volgens de wet van Fitts, worden de moeilijkheid en de tijd om de beweging uit te voeren bepaald door een constante die de relatie weergeeft van de grootte van de doelen ten opzichte van de afstand ertussenin (bewegingsamplitude).

**Hoofdstuk 2** onderzocht of en hoe een selectieve aandoening wat betreft de uitvoering van een actie ook waarneembaar is de perceptie van diezelfde actie. Een neuropsychologische patiënt met een lesie in zijn linker motor schors liet een schending van de wet van Fitts zien in de uitvoering en waarneming van acties. Vanwege de neurale beschadiging, leek het motor systeem van de patiënt niet goed te kunnen omgaan met integratie van informatie voor het uitvoeren van een beweging. We beargumenteren dat de stoornis in het motor systeem de oorzaak is van dezelfde waargenomen schending in de actie waarneming van de patiënt.

**Hoofdstuk 3** beschrijft een functionele kernspintomografie (fMRI) studie waarmee werd onderzocht of de parameters die zuiver motorisch en niet direct

waarneembaar zijn de neurale gebieden aandrijven die uitvoering van acties ondersteunen tijdens de observatie van dezelfde acties in anderen. In eenzelfde actie perceptie paradigma als beschreven in Hoofdstuk 2, werd de graad van de moeilijkheid van de geobserveerde bewegingen (de wet van Fitts) systematisch gemanipuleerd terwijl gecontroleerd werd voor perceptuele aspecten. De resultaten laten een stijging in het BOLD signaal zien in gebieden in het brein die betrokken zijn bij uitvoering van acties in reactie op toenemende motorische moeilijkheid van de geobserveerde bewegingen. Deze gebieden omvatten de primaire motor cortex (M1), de supplementaire motorische schors (SMA), en de globus pallidus van de basale ganglia (BG). Het is essentieel dat de perceptuele aspecten van de geobserveerde bewegingen (oftewel, variërende niveaus van de doelgrootte en de bewegingsamplitude) geen signaalverandering lieten zien in de deze gebieden.

Deze bevindingen, in combinatie met de bevindingen uit Hoofdstuk 2, laten duidelijk zien dat de perceptie van een actie direct gekoppeld is aan de motorische representaties die iemands uitvoering van dezelfde actie bepalen. Het motorische systeem bepaalt niet alleen de uitvoering van de actie, maar is ook direct betrokken bij de actie waarneming alsmede andere manieren van motorische simulaties die de gedetailleerde informatie over motorische paramaters opereren tijdens uitvoering.

**Hoofdstuk 4** beschrijft hoe individuele verwerking beïnvloed wordt door de representatie van iemand anders' doel tijdens sociale interactie. Meer specifiek werd in twee experimenten onderzocht of en hoe de representatie van de taak van een ander tijdens een gezamenlijke taak leidde tot verschillen in informatie tussen proefpersonen tijdens geheugen encoding. Twee proefpersonen voerden een woord categorisatie taak uit. Ze reageerden op de woorden uit de categorieën die individueel aan hun waren toegewezen. De proefpersonen voerden de taak eenmaal alleen uit, en eenmaal samen met hun partner. Daarna werd in een onaangekondigde vrije herinningstaak getest hoe goed ze de woorden onthouden hadden. De resultaten van het eerste experiment lieten zien dat proefpersonen ook items hadden onthouden die toegewezen waren aan hun partner, hoewel deze niet relevant waren voor hun eigen prestatie. In het tweede experiment werd proefpersonen verteld dat ze een geldelijke beloning zouden krijgen om items te

onthouden die tot de hun toegewezen woordcategorie behoorden. In een geleide herinneringstaak werd hun gevraagd om items te herinneren uit alle categorieën. De resultaten waren in overeenstemming met de bevindingen van het eerste experiment en lieten verder zien dat het onthouden van items die niet relevant zijn voor de eigen prestatie, geen negatieve invloed had. Proefpersonen herinnerden items die aan hun partner waren toegewezen hoewel ze hier niet toe aangespoord waren.

**Hoofdstuk 5** beschrijft de toewijzing van gedeelde intenties aan geobserveerde interacties. In een fMRI studie werd onderzocht of sociale interacties die gedreven worden door gedeelde intenties op neurale niveau anders verwerkt worden dan de onafhankelijke acties van meerdere individuen. Met behulp van een observatie paradigma werden videos van handelingen gepresenteerd. De handelingen werden uitgevoerd door twee acteurs en zagen er identiek uit, maar vonden plaats in een verschillende context die bepaalde of de acteurs de actie samen zouden uitvoeren of niet. Voor het zien van de video, luisterden de proefpersonen naar een dialoog tussen de acteurs die de intentionele relaties duidelijk maakte in de daaropvolgende interactie (ofwel een gedeelde intentie ofwel een parallel onafhankelijke intentie). De resultaten lieten zien dat de observaties van interacties gebaseerd op gedeelde intenties zorgden voor verhoogde activatie in hersengebieden zoals de temporale polen, de precuneus en het ventrale striatum in vergelijking met de observaties gebaseerd op parallelle intenties. De precuneus en de temporale polen worden geassocieerd met mentalisatie; het ventrale striatum heeft een specifiekere rol in het ophalen van herinneringen in relatie tot sociale scripts. Mentalisatie gerelateerde computaties spelen daarom ook een belangrijke rol in het identificeren van sociale interacties. De waargenomen activatie in het ventrale striatum, met haar vastgestelde rol in het verwerken van primaire alsmede sociale beloningen, zou een indicatie kunnen zijn van een belonende ervaring in de waarnemer, die veroorzaakt wordt door de observatie van sociale interacties gebaseerd op gedeelde intenties.



## Curriculum Vitae

Terry (Tülin) Eskenazi was born in 1977 in Istanbul. She attended the secondary school at Koç Özel Lisesi and completed her B.A. degree in Psychology at Koç University, Istanbul. There she gained experience in experimental research and investigated text processing in healthy adults as part of her finishing thesis. Following that she continued her studies at the London School of Economics where she attained her M.Sc. degree in Social Psychology. Her dissertation project examined psychosocial factors on the etiology of Anorexia Nervosa. She subsequently took various research jobs at the Universities of Manchester and Birmingham. During which time, she was involved in numerous projects involving a range of topics including biosocial influences on depression, dietary behaviour, and person perception. She also had the opportunity to work with neuropsychological patients in Birmingham.

She paused her academic work to temporarily move back to Istanbul, where she provided consultancy services to NGOs, local governmental organizations as well as private multinational companies based in Turkey. These services provided assistance with developing social responsibility projects and applying for subsidies from a host of funding agencies. She resumed her studies in 2007 at the University of Birmingham and started working with Natalie Sebanz and Guenther Knoblich in Social Cognition, with a particular focus on Joint Action. She moved to the Netherlands in 2008 and started her PhD at the Donders Institute for Brain, Cognition and Behaviour in Nijmegen. In her doctoral research she combined behavioural and neuroimaging methods to study social perception in healthy adults as well as in neuropsychological patients. Since February 2013 she has been working as a post-doctoral fellow with Laurence Conty and Julie Grezes at the École normale supérieure in Paris.



## Publications

### *Peer-reviewed Articles*

**Eskenazi**, T., Rueschemeyer, S-A., de Lange, F., Knoblich, G., & Sebanz, N. (under revision). Observing shared intentions: an fMRI investigation.

**Eskenazi**, T., Doerrfeld, A., Logan, G., Knoblich, G., & Sebanz, N. (2012). Your words are my words: effects of acting together on encoding. *Quarterly Journal of Experimental Psychology*, DOI:10.1080/17470218.2012.725058.

**Eskenazi**, T., Rotshtein, P., Grosjean, M., & Knoblich, G. (2011). The neural correlates of Fitts's law in action observation: an fMRI study. *Social Neuroscience*, 7(1), 30–41.

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### *Book Chapters*

**Eskenazi**, T, van der Wel, R. & Sebanz N. (2012). Mechanisms of Skilled Joint Action Performance. In A. M., Williams & N. J., Hodges (Eds), *Skill Acquisition in Sport: Research, Theory and Practice*, 2nd Edition. Routledge: New York.





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I never thought this part would be the most difficult to write... On the millionth time I sit myself down to write my thanks, once again I am overwhelmed with a sense of gratitude for so many whose grace and generosity touched me in ways that changed me for good and, I hope, for the better... And it is this feeling of gratitude, more than one of pride that marks this momentous event for me.

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July, 2013, Paris.

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